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Influence of the Abundance, Size, and Yolk Reserves of Juvenile Chum Salmon (*Oncorhynchus keta*) on Predation by Freshwater Fishes in a Small Coastal Stream

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Predator–prey interactions between juvenile chum salmon (*Oncorhynchus keta*) and piscivores were studied in a small coastal stream and in sections of a controlled-flow channel. The predators were primarily large (≥100 mm FL) rainbow trout (*Salmo gairdneri*) and large (≥75 mm FL) coho salmon (*O. kisutch*). The relationship between chum salmon fry abundance and the quantity consumed by predators suggested a type II functional response. Neither prey size nor prey abundance influenced predation, but predators did select fry with relatively high yolk reserves. Our results suggest that the numbers of juvenile chum salmon needed to satiate predators and to enhance fry survival are attainable by enhancement projects located on smaller rivers and streams.

On a étudié les interactions prédateur–proie entre de jeunes saumons kétas (*Oncorhynchus keta*) et des espèces piscivores dans un petit cours d'eau côtier et dans des tronçons d'un chenal à débit contrôlé. Les prédateurs étaient surtout de grosses (LF ≥ 100 mm) truites arc-en-ciel (*Salmo gairdneri*) et de gros (LF ≥ 75 mm) saumons cohos (*O. kisutch*). La relation entre l'abondance des alevins de saumon kéta et la quantité consommée par les prédateurs suggérait une réaction fonctionnelle de type II. Ni la taille des proies ni leur abondance n'ont eu d'influence sur la prédation, mais les prédateurs choisissaient des alevins qui avaient des réserves vitellines relativement élevées. Nos résultats portent à croire que le nombre de jeunes saumons kétas nécessaires pour rassasier les prédateurs et améliorer la survie des alevins peut être atteint par des projets de mise en valeur importantes dans de petites rivières et de petits cours d'eau.

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While in streams and lakes, large numbers of juvenile Pacific salmon (*Oncorhynchus* spp.) are eaten by fish, birds, and mammals. Studies have found that freshwater predators can consume up to 85% of the salmon juveniles available to them (Neave 1953; Hunter 1959; Foerster 1968; Ruggerone and Rogers 1984). Many elements influence predation on juvenile salmon, including predator and prey size (Hunter 1959; Bams 1967; Beall 1972), physiological stresses (Sylvester 1971), environmental conditions (Ginetz and Larkin 1976), and relative abundances of predators (Mace 1983) and prey (Peterman and Gatto 1978; Ruggerone and Rogers 1984).

An important factor affecting predation is the functional response of predators to their prey. This response is the relationship between the consumption rate of prey by predators and prey abundance (Solomon 1949; Holling 1959, 1965). Four distinct types of functional responses can occur, each of which forms an asymptote either at the satiation level of the predator or with the time required to handle and consume prey (Holling 1959, 1965; Murdoch and Oaten 1975). Each response also has an associated percent mortality curve that describes the relationship between prey abundance and percent mortality.

Little is known about how predators respond to differing prey densities of salmon. Previous investigations have often not provided enough information on the composition and abundance of predators to reliably measure their functional responses (Peterman and Gatto 1978). Consequently, there are few studies where the functional responses of salmon predators have been empirically measured (Ginetz 1970; Sylvester 1971; Ruggerone and Rogers 1984).

More is known about the types of juvenile salmon selected as prey by freshwater predators. Most studies, however, have only examined the affect of body size on predator selectivity (Bams 1967; Mead and Woodall 1968; Patten 1971, 1977; Ruggerone and Rogers 1984; Taylor and McPhail 1985). Other parameters that may affect which juvenile salmon are eaten by predators, such as the amount of yolk materials that newly emerged fry possess and the abundance of fry, have not been extensively studied.

Here we describe experiments on the functional response and selectivity of freshwater fishes preying on juvenile chum salmon (*O. keta*) fry in a small stream. We wished to (1) ascertain the fish predators of chum fry, (2) measure the functional response and percent mortality relationships between juvenile chum salmon and their predators (3) determine whether predators consume fry on the basis of their size (both length and weight) or yolk amount, and (4) ascertain whether abundance of prey affects predator selectivity. As emphasized by Peterman (1977), Peterman and Gatto (1978), Ruggerone and Rogers (1984), and others, we need to increase our understanding of biological and environmental factors

which affect predation on juvenile salmon. This type of information can help optimize the production of salmon by regulating the quantities and characteristics of juvenile salmon that should be released.

Methods

Study Area

Studies were conducted at the University of Washington Fish Research Station located on Big Beef Creek, Washington, a stream draining into the eastern side of Hood Canal. The stream originates in marshes and beaver ponds, flows 9 km to a 2.5-ha reservoir, and then descends 10 km through a steep canyon to enter Hood Canal. A permanent weir and fish trap that captures all upstream and downstream migrants is located at the mouth of the stream. A portion of Big Beef Creek is diverted 1 km above the weir to provide for a controlled-flow channel. Two identical artificial streams, each 33.3 × 3.3 m, were constructed within the channel. The artificial streams were designed to simulate segments of Big Beef Creek. They were closed systems. Fish could not enter them, and when placed within could only exit through a trap at the lower end.

Experiments

Two separate experiments were conducted. The first involved releasing groups of chum salmon into Big Beef Creek in 1980 and 1981 and then recapturing survivors at the weir after each release. The second consisted of releasing groups of juvenile chum salmon into each artificial stream section in 1982 and recapturing survivors in the fish traps. We used the channel to control water flow and predator movements which we could not manipulate in the stream. In each experiment, juvenile chum salmon migrated downstream past an array of predators. The numbers of juvenile chum released and then subsequently recaptured were used to derive functional response and percent mortality curves. Predator selectivity was evaluated by comparing length and weight of fry and the amount of yolk present before and after their exposure to predators.

Prey

The chum salmon utilized each year were from the same stock and were incubated in the same manner (either within egg boxes or Heath Techna trays supplied with a rugose substrate). Fry were used after they had absorbed most of their yolk reserves, a stage that corresponded to a K_D value (Bams 1970) of approximately 1.85.

Predators

To determine the fish species that eat chum salmon in Big Beef Creek, releases of fry were made into the stream 1.8 km above the weir at dusk on March 22 and 24, 1981. Five to 10 h after each release, potential predators were captured between the point of release and the weir with a Smith-Root Mark VII backpack electroshocker. Electrofishing was done at this time because chum fry rapidly migrate downstream during periods of darkness and thus are exposed to predators for a short period of time. The collected fish were preserved in 10% formalin, and their stomachs were examined for the presence of chum salmon.

To estimate the abundance and size composition of predators within Big Beef Creek, five randomly selected transects, each 33 m in length and located in the lower 1.8 km of the creek, were sampled in 1981. Sampling was conducted on five consecutive days in February, March, and April with the backpack electroshocker; the same transects were used each month. Before electroshocking, a 5-mm-mesh seine was placed at the upper and lower end of the transect. Three passes were made through each transect from the lower to the upper end, and the catch from each pass was saved in separate buckets, counted, measured (salmonids, millimetres fork length; nonsalmonids, millimetres standard length), and then returned to the stream.

The abundance (±95% confidence intervals) of each predator species was estimated using the three pass removal method (Zippin 1958). Estimates of abundance were only made for fish ≥60 mm because we found that smaller fish were incapable of consuming chum fry. The population size of each species in the lower 1.8 km of Big Beef Creek was ascertained by calculating the average number of predators in the five transects and multiplying this value by 55 (the number of 33-m-long segments in the lower 1.8 km of the creek). Also, separate estimates of the number of small and large individuals were made for the two most abundant species, coho salmon (*O. kisutch*) and rainbow trout (*Salmo gairdneri*). Rainbow trout 60–99 mm were classified as small and those ≥100 mm were classified as large. For coho salmon, small fish were <75 mm (the modal length) and large fish were ≥75 mm. We estimated the number of chum eaten by each predator species by multiplying the number of specimens of each predator found in the lower 1.8 km of the creek by the average number of chum found in the stomachs of that species following the two releases in March 1981. This procedure accounts for the number of fry eaten 5–10 h after a release. Because >90% of the fry in a release group exited Big Beef Creek during this time, our estimates considered most of the predation that occurred.

Big Beef Creek releases

In 1980, five groups of chum fry, ranging from 517 to 50 155 individuals, were released 2.3 km above the weir (Table 1). In 1981, seven groups of fry, ranging from 817 to 31 441 individuals, were released 1.8 km above the weir (Table 1). These releases were made 1.5 h before sunset in 1980 and 2.0 h before sunset in 1981, and the order of release was random (Table 1). All releases were made in March, a time when chum fry are normally emigrating from the stream. However, to eliminate the chance that wild fry would inflate the numbers of chum available to predators, we prevented chum salmon from spawning in Big Beef Creek.

Field experiments (Phinney and Mathews 1969; Phinney 1974; S. L. Schroder, unpubl. data) have shown that juvenile salmon marked with fluorescent pigments retain the marks for extended periods and escape predation at the same rate as unmarked controls. Therefore, we used these pigments to distinguish our different release groups. Approximately 48 h after a group was marked, the dead were counted, removed, and a subsample of at least 250 fry was retained. The remaining fish were transported to the release location, acclimated to the stream for at least 1 h, additional dead were removed, and the rest were released. Thus, for each group, the total number of fry released was the number to be marked minus both the number retained in the subsample and all mortalities. At least 100 fish in each subsample were measured (millimetres), weighed (to the nearest 0.01 g), and examined for the presence of pigment (to determine the proportion marked). The number

TABLE 1. Summary of the release characteristics of each group of chum salmon fry released into Big Beef Creek in March 1980 and 1981.

Year	Date released in March	Time released	No. released	Pigment retention (%)[a]	Fork length (mm) at release		Weight (g) at release		Condition factor (K_D)[b] at release	
					Mean	SD	Mean	SD	Mean	SD
1980	20	17:05	4 727	71.5	39.4	1.3	0.36	0.07	1.80	0.09
	23	17:10	15 186	62.6	40.2	1.3	0.39	0.04	1.82	0.04
	26	17:05	50 155	52.7	39.1	1.3	0.36	0.04	1.82	0.03
	30	17:06	517	65.9	39.0	0.9	0.36	0.03	1.82	0.03
	31	17:08	1 206	68.4	38.8	0.9	0.34	0.03	1.80	0.04
1981	6	16:02	1 661	83.4	39.8	1.3	0.36	0.05	1.79	0.05
	8	16:09	4 061	73.5	38.7	1.7	0.34	0.05	1.80	0.07
	10	16:10	15 431	86.3	39.1	1.4	0.34	0.05	1.78	0.05
	12	16:12	31 441	86.6	39.4	1.5	0.34	0.04	1.76	0.04
	14	16:14	817	82.1	38.2	1.5	0.33	0.05	1.80	0.04
	16	16:16	1 669	93.8	38.3	1.4	0.33	0.04	1.79	0.04
	18	16:15	3 887	96.1	38.4	1.7	0.32	0.05	1.78	0.05

[a]Percent of fish released that retained pigment.
[b]K_D = a measure of the relative amount of yolk materials the fry possess (after Bams 1970).

TABLE 2. Summary of the characteristics of each group of chum salmon fry released into the artificial stream sections of the Big Beef Creek channel in 1982.

Date of release	Time of release	No. released		Fork length (mm) at release		Weight (g) at release		Condition (K_D)[a] at release	
		Section 2	Section 3	Mean	SD	Mean	SD	Mean	SD
March 27	19:12	100	1095	39.6	1.3	0.39	0.04	1.84	0.04
March 30	19:15	250	40	39.5	1.9	0.39	0.05	1.85	0.05
April 1	19:16	40	400	38.9	1.8	0.37	0.04	1.84	0.07
April 4	19:18	750	100	39.4	1.4	0.37	0.03	1.82	0.05
April 6	19:20	100	750	39.4	1.4	0.37	0.04	1.80	0.04
April 8	19:22	400	—	39.1	1.7	0.35	0.04	1.80	0.06
April 10	19:24	400	250	38.9	1.8	0.35	0.04	1.81	0.07
April 12	19:27	1100	—	39.4	1.4	0.37	0.05	1.82	0.04
April 14	19:26	40	750	39.1	1.8	0.36	0.05	1.82	0.05

[a]K_D = a measure of the relative amount of yolk materials the fry possess (after Bams 1970).

of marked fry in a release group was estimated by multiplying the percentage of the fish marked in the subsample by the total number released.

The fish traps at the weir were monitored every 0.5 h during the 8 h immediately following a release and at 2-h intervals at other times. When less than 4000 fry were released, all the recaptured fish were examined for pigment and a subsample of approximately 100 chum was measured and weighed. When more than 4000 fish were released, a random sample of at least 1000 recaptured fry was examined for pigment and a subsample of about 100 fish was measured and weighed.

Artificial stream sections

Predators were obtained from Big Beef Creek and placed in the artificial stream sections several weeks before fry releases. The number and size of fish placed in each section were similar to that found in a 33-m-long section of the creek in March 1981.

Nine releases of chum fry were made into each artificial stream section between March 27 and April 14, 1982 (Table 2). Six different densities of chum fry were released, three of which were replicated, and the order of releases in each section was randomly determined. None of these groups were marked because we found that they migrated rapidly through the sections after release (K. L. Fresh and S. L. Schroder, unpubl. data). The fry were held without food in a tank for 48 h prior to their scheduled release, counted, placed in containers at the upstream end of a section to acclimate for at least 1 h, and released at sunset. An additional 100 fry from the holding tank for each release were measured and weighed. Chum captured in the traps at the base of each section were removed and counted. When less than 100 chum fry were released, all fry recaptured within 24 h were measured and weighed; for larger releases, a random subsample of 100 fish was similarly treated.

Functional Response and Percent Mortality Curves

For each series of releases, functional response and percent mortality curves were derived by plotting the number or percentage of fry lost within 48 h against the number released. This time period was selected because we found that >97% of the fry exited the creek or channel sections within 2 d (K. L. Fresh and S. L. Schroder, unpubl. data).

We assumed that all groups within any one set of releases were exposed to the same predator population (i.e. predator abundance was constant and growth was insignificant). Thus it was not necessary to account for the number of predators for each release. We designed our experiments to reduce the

TABLE 3. Consumption of juvenile chum salmon by predators in lower Big Beef Creek following the release of fry on March 22 and 24, 1981.

	Estimated population size[a]		No. of stomachs examined	No. with chum	No. of chum/stomach		Estimated no. of chum eaten
	Numbers	±95% C.I.			$\bar{x}$	SD	
March 22, 1981							
Coho salmon (small)	737	319	34	9	0.38	0.74	280
Coho salmon (large)	605	262	31	13	0.94	1.28	569
Rainbow trout (small)	291	86	20	4	0.40	1.14	116
Rainbow trout (large)	187	55	10	7	6.50	6.80	1215
Cutthroat trout[b]	31	—	4	2	3.00	—	93
Prickly sculpin	354	192	20	3	0.30	—	106
Coastrange sculpin	312	166	35	1	0.03	—	10
Total	2517	1080					2389
March 24, 1981							
Coho salmon (small)	703	304	42	9	0.31	0.68	218
Coho salmon (large)	574	249	27	10	1.37	2.30	786
Rainbow trout (small)	271	80	15	3	0.28	0.60	76
Rainbow trout (large)	177	51	8	8	6.00	4.60	1062
Cutthroat trout[b]	30	—	4	2	3.00	—	90
Prickly sculpin	334	171	15	0	0	—	0
Coastrange sculpin	277	147	18	1	0.06	—	17
Total	2366	1002					2249

[a]From the March 9–13, 1981, electroshocking survey. The number of predators in the lower 1.8 km on March 24 was estimated as the number in the section on March 22 minus the number removed for stomach contents analysis on March 22; C.I. = confidence interval.

[b]Data for cutthroat trout were combined for the two releases because of the small sample size.

likelihood that changes in predator abundance would occur. The weir prevented predators from moving upstream into our study area, and to reduce the possibility of downstream movements our studies took place in late winter. At this time, the instream movements of overwintering salmonids are considered to be minimal (e.g. Salo 1955; Tschaplinski and Hartman 1983). Studies by Seiler et al. (1984) in Big Beef Creek support this belief, as they found that peak catches of wild coho salmon and trout smolts at the weir occurred after March. We also made our releases at a time when temperatures and food (i.e. invertebrates) were low and over a short time period (<20 d) to reduce the possibility of predator growth. Release and recovery of 111 tagged predators in Big Beef Creek (K. L. Fresh and S. L. Schroder, unpubl. data) verified that predators remained in the same locations and that their growth was minimal during the course of our experiments.

Selective Predation

We analyzed predator selectivity for each release with respect to fry length, weight, and the amount of yolk (i.e. K_D values, Bams 1970). Predator selectivity data were restricted to fish recovered within 24 h after release, and only data from marked recoveries from Big Beef Creek were used. We measured the frequency distributions of each variable before and after release by the Kologmorov–Smirnov test (Zar 1974), and where there were significant differences, the direction of the difference was determined graphically.

To test the hypothesis that the abundance of chum fry influenced prey choice, we utilized an index of selection intensity (S) modified from Bartell (1982). This was calculated as the difference in the mean value of a parameter (i.e. length, weight, or K_D) at release and at recapture ($\bar{x}$ release $-$ $\bar{x}$ recapture) divided by the overall range of the parameter. Bartell (1982) stated that parameter values more than two standard deviations from the mean can unduly influence this index; thus these extremes were eliminated for each calculation of S. The index S ranges between -1 and $+1$ with values near 0 indicating no size selection. Spearman rank correlations were computed between S and chum abundance to evaluate relationships between the abundance of chum and selection intensity.

Results

Predator Population in Big Beef Creek

Three salmonids (coho salmon, rainbow trout, and cutthroat trout (*Salmo clarki*)) and two cottids (coastrange sculpin (*Cottus aleuticus*) and prickly sculpin (*C. asper*)) were found to eat chum fry (Table 3). Another fish species found in Big Beef Creek, the shorthead sculpin (*C. confusus*), is large enough to feed on chum salmon juveniles and will do so under laboratory conditions (K. L. Fresh and S. L. Schroder, unpubl. data) but apparently not in the field. Rainbow trout had the highest occurrence of chum in their stomachs (42%) and the greatest number of chum per predator (2.35 chum), followed by coho salmon and prickly sculpin. Less than 6% of the cottids examined had consumed any chum (Table 3).

Estimates made in March 1981 indicated that the most abundant predator was coho salmon (53% of the estimated 2517 predators), followed by rainbow trout (19%), prickly sculpin (14%), coastrange sculpin (12%), and cutthroat trout (2%). Rainbow trout accounted for just over 50% of the chum consumed following the releases on March 22 and 24, 1981, while coho ate 35 and 45%, respectively (Table 3). Cutthroat

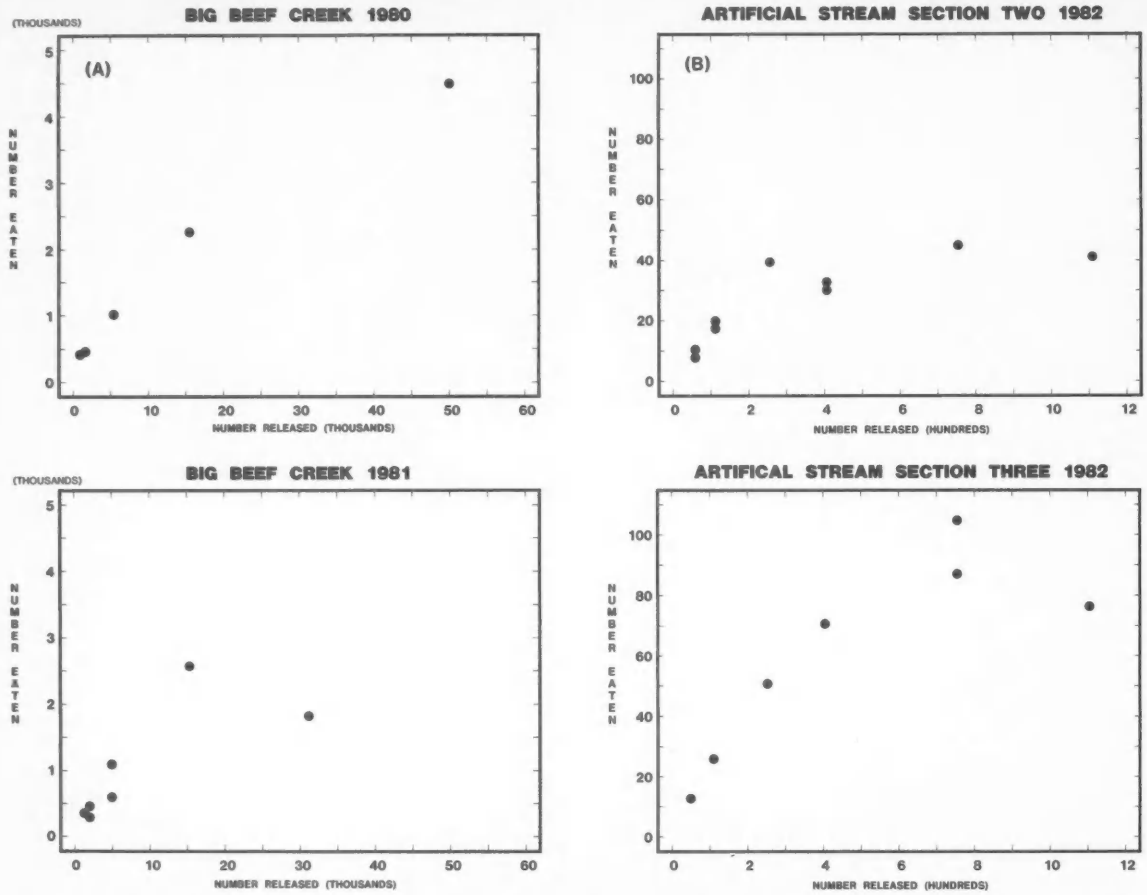

FIG. 1. Number of chum salmon fry eaten by piscivores in (A) Big Beef Creek plotted against the number of fry released in 1980 (top) and 1981 (bottom) and (B) artificial stream section 2 (top) and section 3 (bottom) plotted against the number of fry released in 1982.

trout, prickly sculpin, and coastrange sculpin ate only a small percentage of the chum. Even though large coho and large rainbow trout were much less abundant than their smaller conspecifics, together they were responsible for 75% of the predation on March 22 and 82% on March 24 (Table 3).

Functional Response

In all cases, the number of salmon eaten increased asymptotically (Fig. 1). The data are best described by type II and type III functional responses. Examination of the mortality curves (Fig. 2) indicates that they best fit a type II response except for the 1981 stream release which could also be fitted by a type III curve.

Chum Selection by Predators

The predators did not appear to consistently select chum on the basis of either their length or weight (Table 4). Small or large chum were preferentially selected in only 8 of the 25 tests; in four cases the larger chum were selected whereas in the other four, smaller chum were chosen. In 11 of 25 tests, chum were selected on the basis of weight, but again there was no consistent pattern shown (Table 4). Sixteen of the 25 Kologmorov–Smirnov tests that measured changes in yolk reserves (K_D values of fry) were significant ($p < 0.10$); 13 indicated selection for relatively high K_D values, 2 for low K_D values, and in 1 there was no apparent pattern.

The degree of selective predation did not appear to be related to the abundance of chum. Only one of the Spearman correlations comparing selection intensity and abundance of chum for the three parameters examined (length in 1980; $r = 1.00$, $p < 0.05$, $n = 4$) was significant. Most values of S ranged between -0.1 and $+0.1$ (Table 4), regardless of the experiment or the parameter tested.

Discussion

Predators of Chum Fry in Big Beef Creek

Most of the predation on chum salmon fry in Big Beef Creek was by large rainbow trout and large coho salmon. Consequently, our evaluation of predator functional response, percent mortality of chum fry, and selectivity applies mainly to these predators. Both species are major predators of juvenile salmonids in freshwater (Hunter 1959; Ward and Larkin 1964;

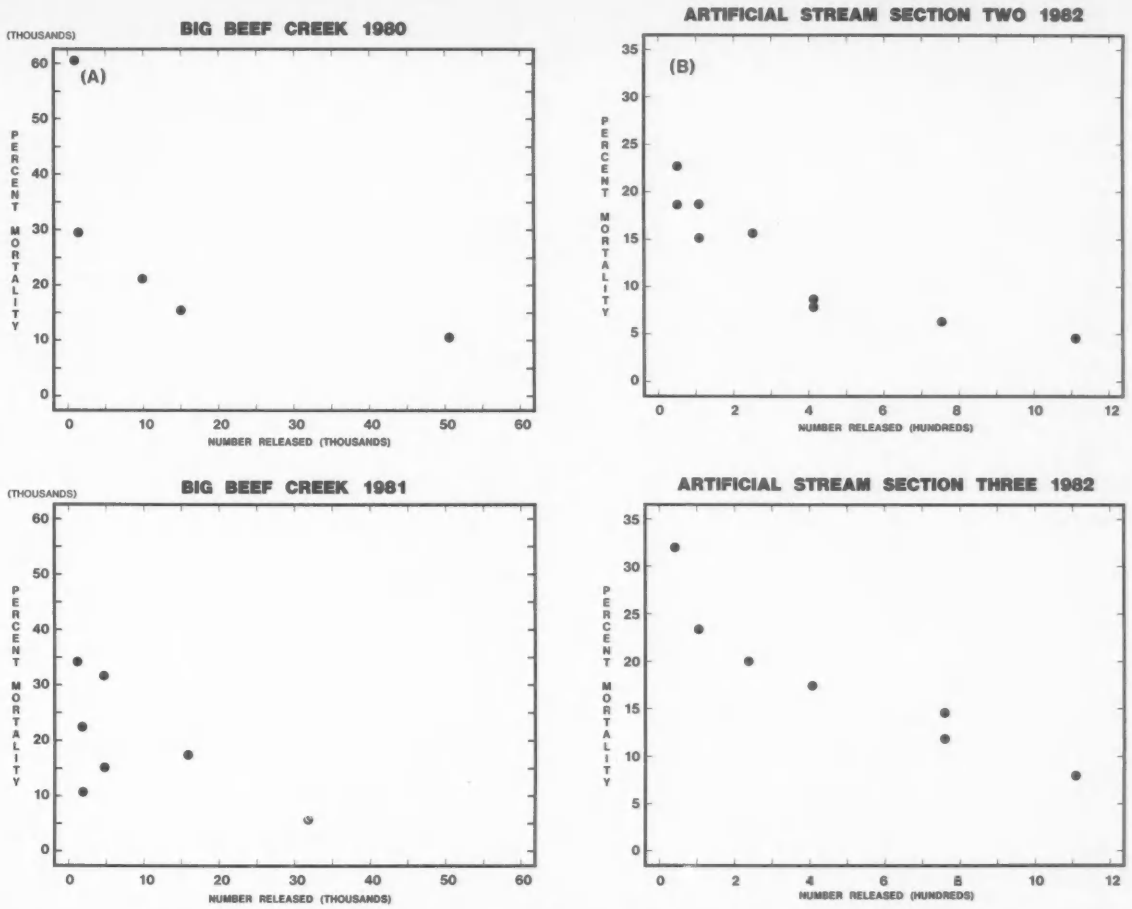

FIG. 2. Percent mortality of chum salmon fry plotted against the number of fry released into (A) Big Beef Creek in 1980 (top) and 1981 (bottom) and (B) artificial stream section 2 (top) and section 3 (bottom) in 1982.

McCart 1967; Foerster 1968; Patten 1972). Rainbow trout have been primarily implicated as predators of juvenile sockeye salmon (*O. nerka*) but their predation on juvenile chum salmon has not been well documented. This may be because rainbow trout are often less abundant than other predators (e.g. coho salmon and sculpins). Our results suggest that in streams where chum and rainbow trout occur together, rainbow trout should be included in investigations of predation. Similarly, studies of predation on juvenile salmon should also include the quantity of fish consumed by larger, rarer predators, as our findings suggest that much of the predation may be by these individuals. There are several reasons why such fish can consume substantial quantities of juvenile salmon. Visual acuity, swimming speed, and mouth size all increase with fish growth; therefore, larger fish can more readily locate, pursue, capture, and consume juvenile salmon. Additionally, as stream-dwelling salmonids increase in size, they typically move into areas associated with progressively higher water velocities (Lister and Genoe 1970; Everest and Chapman 1972). Since fry tend to migrate downstream in areas of faster currents (Hoar 1951; S. L. Schroder and K. L. Fresh, unpubl. data), large predators may encounter more fish than smaller conspecifics.

Regardless of their body size, sculpins were not significant predators of chum salmon fry in Big Beef Creek. These results are consistent with most other investigations of sculpin predation (see review by Moyle 1977) which suggest that sculpins are not important predators of juvenile salmon except where the fish are concentrated into relatively small areas.

Functional Response and Percent Mortality

The predators of chum salmon fry in Big Beef Creek exhibited a type II functional response in three of four tests and either a type II or type III response in one test (the 1981 stream releases). The type II curve occurred under our most controlled conditions (i.e. artificial stream sections) and, therefore, probably best represents the response of the predators we examined. A type II response occurs when prey are most vulnerable at low abundance and least vulnerable when it is high. The decrease in vulnerability at high prey levels generally results from predator satiation or from time constraints arising from handling and swallowing prey (Holling 1959, 1965; Murdoch and Oaten 1975).

The distinction between a type II and III response curve has significant implications for the management of salmonid popu-

TABLE 4. Selection of chum salmon by predators on the basis of length, weight, and condition (the relative amount of yolk as measured by K_D) during creek and artificial stream releases, 1980–82. The relationship between chum abundance and predator selectivity is given by $S = ((\bar{x}$ at release $- \bar{x}$ at recapture)/parameter range).

Group and no. released[a]	Length[b]				Weight[b]				K_D[b]			
	d	*n*	Sign.	*S*	*d*	*n*	Sign.	*S*	*d*	*n*	Sign.	*S*
Stream, 1980												
50 155	0.210	50	0.05	0.10	0.264	50	0.05	0.16	0.226	50	0.05	0.04
15 186	0.200	50	0.05	0.09	0.240	50	0.05	0.11	0.160	50	ns	0
1 206	0.156	50	ns	−0.06	0.214	50	0.05	−0.08	0.196	50	0.05	−0.08
517	0.083	51	ns	−0.08	0.146	51	ns	0.08	0.215	51	0.05	0.08
Stream, 1981												
31 441	0.086	195	0.10	0.03	0.062	195	ns	0.05	0.054	195	ns	0
15 431	0.065	105	ns	0.02	0.082	105	ns	0	0.140	105	0.05	−0.04
4 061	0.255	100	0.05	−0.07	0.066	50	ns	0	0.256	50	0.05	0.07
3 887	0.099	170	0.05	−0.05	0.101	170	0.05	−0.05	0.118	170	0.05	−0.06
1 669	0.058	123	ns	−0.03	0.096	123	ns	0	0.222	123	0.05	0.11
1 661	0.236	50	0.05	0.13	0.264	50	0.05	0.10	0.178	50	0.10	0
817	0.188	144	0.05	−0.07	0.056	144	ns	−0.05	0.174	144	0.05	0.16
Channel section 3, 1982												
750	0.110	100	ns	−0.01	0.100	100	ns	0.05	0.180	100	0.05	0.09
750	0.040	100	ns	−0.02	0.190	100	0.05	0.10	0.250	100	0.05	0.10
400	0.190	100	0.05	−0.08	0.130	100	0.10	−0.05	0.080	100	ns	0
250	0.050	100	ns	−0.01	0.080	100	ns	0	0.080	100	ns	0.04
100	0.065	71	ns	−0.04	0.106	71	ns	0	0.068	71	ns	0
40	0.231	26	ns	−0.07	0.135	26	ns	0.05	0.212	26	ns	0.10
Channel section 2, 1982												
1 100	0.050	100	ns	−0.02	0.210	100	0.05	0.05	0.360	100	0.05	0.16
750	0.080	100	ns	−0.04	0.080	100	ns	0	0.130	100	0.10	0.05
250	0.110	100	ns	0.04	0.230	100	0.05	0.09	0.222	100	0.05	0.09
100	0.058	79	ns	−0.02	0.230	79	0.05	0.14	0.275	79	0.05	0.13
400	0.100	100	ns	−0.06	0.160	100	0.05	−0.06	0.060	100	ns	0
400	0.090	100	ns	−0.07	0.080	100	ns	0	0.180	100	0.05	0.07
40	0.143	30	ns	0.01	0.147	30	ns	0.05	0.150	30	ns	0.05
40	0.140	30	ns	−0.04	0.090	30	ns	−0.05	0.117	30	ns	0.03

[a]Recovery measurements were not obtained for the release of 4727 fish in 1980 and for the artificial stream section releases on March 27, 1982.
[b]d = calculated d value from Kologmorov–Smirnov test, n = sample size, sign. = significance of test (0.05 = significant at $p < 0.05$; 0.10 = significant at $p < 0.10$; ns = not significant, i.e. at $p \geq 0.10$).

lations. A type III relationship occurs when percent mortality increases with prey abundance up to a threshold level, after which mortality decreases (assuming a constant number of predators). Therefore, it is necessary to increase juvenile salmon abundance above this threshold value to increase their survival. In the type II response, survival increases until the predator population is consuming all the prey it can within a given amount of time. Our results suggest that this level of satiation may be relatively low (Fig. 1 and 2), one that can be attained by chum salmon enhancement programs (e.g. hatcheries, streamside egg incubation boxes, or spawning channels) established in small rivers and streams.

Selective Predation

In contrast with most other comparable studies (e.g. Mead and Woodall 1968; Patten 1971; Beall 1972; Taylor and McPhail 1985), our results showed that predators in Big Beef Creek were not size selective. There are several possible reasons for this. First, we examined a number of fish species, each represented by various size ranges. Other studies that have tested for selective predation have looked at a single predator species represented by individuals having approximately the same body size. Smaller predators in Big Beef Creek may have fed in a selective fashion; however, this would have been obscured if the larger fish (responsible for most of the predation) consumed fry nonselectively. The bioenergetic costs accrued by larger fish as they pursue, capture, and consume individual fry within the size range (35–44 mm) that we released may be fairly equivalent. Hence, regardless of fry density, these fish may not need to selectively capture prey in order to optimize caloric profits.

A second explanation may be that another variable or variables other than size had a more important influence on which fry were eaten. Bams (1967), for instance, suggested that fry that have absorbed most of their yolk materials should not be as vulnerable to predators as those carrying larger amounts of yolk. Our results support this notion, since we found that predators had a proclivity to select fry that possessed relatively high K_D values. These fish may have been more vulnerable than more developed fry because the yolk created a hydrodynamic drag that reduced their swimming speed (Bams 1967), or their orange–red yolks may have made them more visible to predators. In addition, predators may have "sought

out" such fish because of the bonus calories contained within their yolks.

In two cases, however, we found that predators had selectively eaten fish with relatively low K_D values. Many of the fry released in these two instances had developed past the point of optimal yolk absorption (i.e. had K_D values < 1.80) and were somewhat emaciated. Thus, their swimming abilities were also probably impaired (Bams 1967), making them more vulnerable to predators because they were less able to avoid them.

The results of this study suggest that freshwater predation on small emigrating chum fry may be reduced by releasing large numbers into the environment over a short time period. The levels needed to satiate predators and minimize freshwater mortality appear to be achievable by enhancement projects located on small rivers and streams. However, management strategies that alter release schedules must be tempered by the needs of the fish after they arrive in estuarine and lacustrine habitats. Fish with large amounts of yolk are particularly vulnerable to predators and thus should not be liberated from an enhancement project.

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References

Bams, R. A. 1967. Differences in performance of naturally and artificially propagated sockeye salmon migrant fry, as measured with swimming and predation tests. J. Fish. Res. Board Can. 24: 1117–1153.

1970. Evaluation of a revised hatchery method tested on pink and chum salmon fry. J. Fish. Res. Board Can. 27: 1429–1452.

Bartell, S. M. 1982. Influence of prey abundance on size-selective predation by bluegills. Trans. Am. Fish. Soc. 111: 453–461.

Beall, E. P. 1972. The use of predator–prey tests to assess the quality of chum salmon *Oncorhynchus keta* fry. M.S. thesis, University of Washington, Seattle, WA. 105 p.

Everest, F. H., and D. W. Chapman. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. J. Fish. Res. Board Can. 29: 91–100.

Foerster, R. E. 1968. The sockeye salmon (*Oncorhynchus nerka*). Bull. Fish. Res. Board Can. 162: 422 p.

Ginetz, R. 1970. Predator–prey interactions that affect survival of migrant sockeye salmon (*Oncorhynchus nerka*) fry. B.S. thesis, University of British Columbia, Vancouver, B.C. 37 p.

Ginetz, R., and P. A. Larkin. 1976. Factors affecting rainbow trout (*Salmo gairdneri*) predation on migrant fry of sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 33: 19–24.

Hoar, W. S. 1951. The behavior of chum, pink and coho salmon in relation to their seaward migration. J. Fish. Res. Board Can. 8: 241–263.

Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can. Entomol. 91: 293–320.

1965. The functional response of predators to prey density and its role in mimicry and population regulation. Mem. Entomol. Soc. Can. 45: 1–60.

Hunter, J. G. 1959. Survival and production of pink and chum salmon in a coastal stream. J. Fish. Res. Board Can. 16: 835–886.

Lister, D. B., and M. S. Genoe. 1970. Stream habitat utilization by cohabiting underyearlings of chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Big Qualicum River, British Columbia. J. Fish. Res. Board Can. 27: 1215–1224.

Mace, P. M. 1983. Bird predation on juvenile salmonids in the Big Qualicum Estuary, Vancouver Island. Can. Tech. Rep. Fish. Aquat. Sci. 1176: 79 p.

McCart, P. 1967. Behavior and ecology of sockeye salmon fry in the Babine River. J. Fish. Res. Board Can. 24: 375–428.

Mead, R. W., and W. Woodall. 1968. Comparison of sockeye salmon fry produced by hatcheries, artificial channels, and natural spawning areas. Int. Pac. Salmon Fish. Comm. Prog. Rep. No. 20: 41 p.

Moyle, P. B. 1977. In defense of sculpins. Fisheries 2: 20–23.

Murdoch, W. W., and A. Oaten. 1975. Predation and population stability, p. 1–131. *In* A. MacFayden [ed.] Advances in ecological research. Vol. 9. Academic Press, London.

Neave, F. 1953. Principles affecting the size of pink and chum salmon populations in British Columbia. J. Fish. Res. Board Can. 9: 450–491.

Patten, B.G. 1971. Predation by sculpins on fall chinook salmon, *Oncorhynchus tshawytscha*, fry of hatchery origin. U.S. Natl. Mar. Fish. Serv. Spec. Sci. Rep. Fish. No. 621: 14 p.

1972. Predation, particularly by sculpins, on salmon fry in freshwaters of Washington. Natl. Tech. Inf. Serv. No. COM-72-10527: 21p.

1977. Body size and learned avoidance as factors affecting predation on coho salmon, *Oncorhynchus kisutch*, fry by torrent sculpin, *Cottus rhotheus*. Fish. Bull. 75: 457–459.

Peterman, R. M. 1977. A simple mechanism that causes collapsing stability regions in exploited salmonid populations. J. Fish. Res. Board Can. 34: 1130–1142.

Peterman, R. M., and M. Gatto. 1978. Estimation of functional responses of predators on juvenile salmon. J. Fish. Res. Board Can. 35: 797–808.

Phinney, D. E. 1974. Growth and survival of fluorescent-pigment marked and finclipped salmon. J. Wildl. Manage. 38: 132–137.

Phinney, D. E., and S. B. Mathews. 1969. Field test of fluorescent pigment marking and finclipping of coho salmon. J. Fish. Res. Board Can. 26: 1619–1624.

Ruggerone, G. T., and D. E. Rogers. 1984. Arctic char predation on sockeye salmon smolts at Little Togiak River, Alaska. Fish. Bull. 82: 401–410.

Salo, E. O. 1955. Silver salmon, *Oncorhynchus kisutch*, survival studies at Minter Creek, Washington. Ph.D. dissertation, University of Washington, Seattle, WA.

Seiler, D., S. Neuhauser, and M. Ackley. 1984. Upstream/downstream salmonid trapping project, 1980–1982. Wash. Dep. Fish. Prog. Rep. No. 200: 152 p.

Solomon, M. E. 1949. The natural control of animal populations. J. Anim. Ecol. 18: 1–35.

Sylvester, J. R. 1971. Some effects of thermal stress on the predator–prey interaction of two salmonids. Ph.D. dissertation, University of Washington, Seattle, WA. 103 p.

Taylor, E. B., and J. D. McPhail. 1985. Burst swimming and size-related predation of newly emerged coho salmon (*Oncorhynchus kisutch*). Trans. Am. Fish. Soc. 114: 546–551.

Tschaplinski, P. J., and G. Hartman. 1983. Winter distribution of juvenile coho salmon (*Oncorhynchus kisutch*) before and after logging in Carnation Creek, British Columbia, and some implications for overwinter survival. Can. J. Fish. Aquat. Sci. 40: 452–461.

Ward, F. J., and P. A. Larkin. 1964. Cyclic dominance in Adams River sockeye salmon. Int. Pac. Salmon Fish. Comm. Prog. Rep. No. 11: 115 p.

Zar, J. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ. 620 p.

Zippin, C. 1958. The removal method of population estimation. J. Wildl. Manage. 22: 82–90.

Adaptive Variation in Body Size, Age, Morphology, Egg Size, and Developmental Biology of Chum Salmon (*Oncorhynchus keta*) in British Columbia

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Beacham, T. D., and C. B. Murray. 1987. Adaptive variation in body size, age, morphology, egg size, and developmental biology of chum salmon (*Oncorhynchus keta*) in British Columbia. Can. J. Fish. Aquat. Sci. 44: 244–261.

Chum salmon (*Oncorhynchus keta*) stocks in British Columbia spawning from August through January and in rivers of different size were surveyed for variation in sex ratios, age composition, meristic characters, morphology, and developmental biology. Males were more abundant than females at the younger (2 and 3 yr of age) and older (5 and 6 yr of age) age-classes. Males had larger heads, thicker caudal peduncles, and larger dorsal fins than did females, but females had larger anal fins than did males. Stocks from large rivers had larger heads, thicker caudal peduncles, and larger fins than did those from small rivers. Chum salmon in an area characterized by a lower number of gillrakers also had a lower number of branchiostegal rays. At the same incubation temperature, alevin hatching time was similar for all stocks examined except those from the Queen Charlotte Islands, which was later than the other stocks. Early-spawning stocks had older fish, larger eggs, and later times of fry emergence than did late-spawning stocks. Late-spawning stocks had higher survival rates of embryos at 4°C than did early-spawning ones. Stocks had different trends in alevin and fry length and weight with respect to incubation temperature. Northern stocks were more efficient than southern stocks at converting egg yolk to fry body weight at low incubation temperatures (4°C). Selection has produced stocks adapted to the various environments that they encounter in their natal streams, allowing chum salmon to exploit a wide variety of spawning habitats in British Columbia.

On a étudié des stocks de saumon kéta (*Oncorhynchus keta*) en Colombie-Britannique qui frayent d'août à janvier et dans des rivières de diverses tailles, pour voir la variation dans le rapport des sexes, la composition par âge, les caractères méristiques, la morphologie et la biologie du développement. Il y avait plus de mâles que de femelles dans les classes d'âge jeunes (âges de 2 et 3 ans) et vieilles (âges de 5 et 6 ans). Les mâles avaient une plus grosse tête, un pédoncule caudal plus épais et des nageoires dorsales plus grandes que les femelles, mais les femelles avaient des nageoires anales plus grandes que les mâles. Les individus de stocks provenant de rivières importantes avaient une tête plus grosse, un pédoncule caudal plus épais et des nageoires plus grandes que ceux provenant de petites rivières. Dans un secteur où les saumons kétas étaient caractérisés par un nombre inférieur de branchiospines, le nombre de rayons branchiostèges était également plus faible. À la même température d'incubation, le temps d'éclosion des alevins était semblable pour tous les stocks examinés sauf pour ceux provenant des îles Reine-Charlotte, où le temps d'éclosion était plus tardif que pour les autres stocks. Dans les stocks qui frayaient tôt, les poissons étaient plus vieux, les oeufs plus gros et la sortie des alevins se produisait plus tard que dans les stocks qui frayaient tard. Chez ces derniers, le taux de survie des embryons à 4°C était plus élevé que chez les premiers. On a remarqué dans les stocks des tendances différentes dans la longueur et le poids des alevins par rapport à la température d'incubation. Les stocks du nord étaient plus efficaces que les stocks du sud pour convertir le vitellus en poids corporel d'alevins à de basses températures d'incubation (4°C). La sélection a produit des stocks adaptés aux divers milieux qu'ils rencontrent dans leurs cours d'eau natals, permettant aux saumons kétas d'exploiter une grande variété d'habitats propices à la reproduction en Colombie-Britannique.

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Pacific salmon vary considerably in age and size at maturity, morphology, and timing of spawning. However, at maturity, they return to spawn in their natal streams at specific times, and this segregation of spawning adults in both location and time leads to the existence of discrete stocks, where a stock is considered as the members of a particular spawning population (Ricker 1972). Stocks may be genetically adapted for their particular spawning locations and times (Raleigh 1967; Ricker 1972), and differences among stocks may be adaptations to different spawning, incubation, and rearing environments.

In British Columbia, chum salmon (*Oncorhynchus keta*) spawn in over 880 rivers and streams (Aro and Shepard 1967), with the spawning habitat ranging from tidal areas, to small streams only a few kilometres in length, to the mainstems of large rivers over 200 km from salt water. Spawning may occur

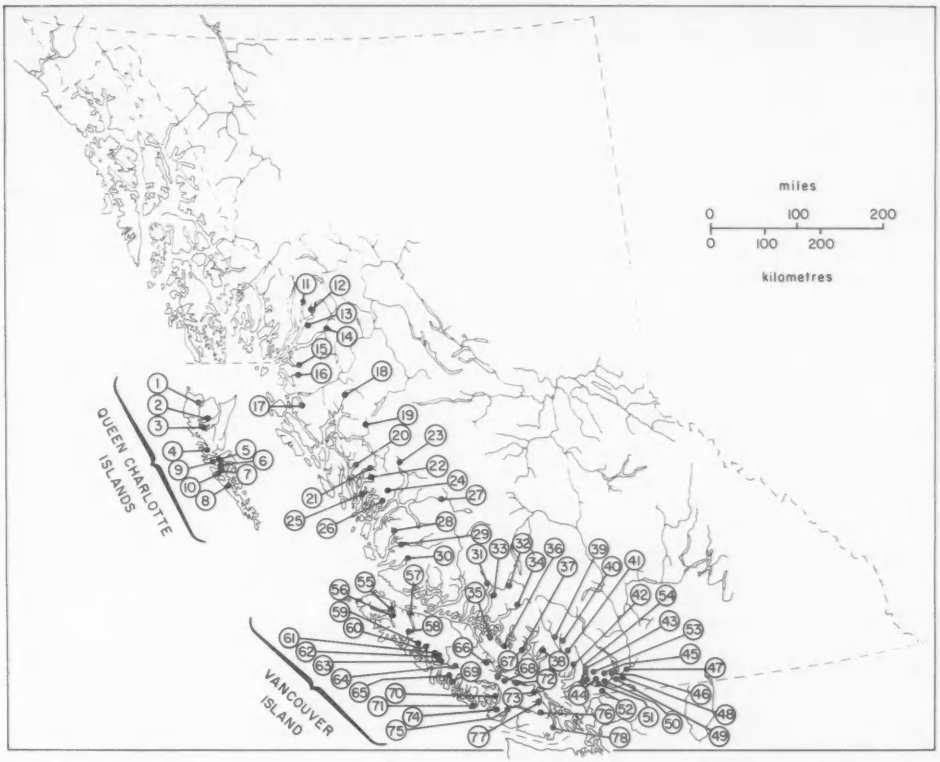

FIG. 1. Locations where chum salmon were sampled during 1981–85. Queen Charlotte Islands: (1) Stanley Cr., (2) Ain R., (3) Awun R., (4) Lagins Cr., (5) Deena Cr., (6) Pallant Cr., (7) Lagoon Cr., (8) Salmon R., (9) Security Cr., (10) Tasu Cr., North coast: (11) Kshwan R., (12) Kitsault R., (13) Stagoo R., (14) Nass R., (15) Khutzeymateen R., (16) Toon R., (17) Ecstall R. Central coast: (18) Kitimat R., (19) Kemano R., (20) Green R., (21) Mussel R., (22) Kainet Cr., (23) Kimsquit R., (24) Cascade R., (25) Neekas Cr., (26) Elcho Cr., (27) Bella Coola R., (28) Clyak R., (29) Wannock R., (30) Nekite R. South coast: (31) Homathko R., (32) Southgate R., (33) Orford R., (34) Toba R., (35) Okeover Cr., (36) Sliammon R., (37) Saltery Bay Cr., (38) Tzoonie R., (39) Squamish R., (40) Cheakamus R., (41) Mamquam R., (42) Indian R. Fraser River: (43) Alouette R., (44) Chilqua Cr., (45) Chehalis R., (46) Weaver Cr., (47) Fraser R., (48) Wahleach R., (49) Harrison R., (50) Squakum Cr., (51) Inch Cr., (52) Vedder R., (53) Stave R., (54) Blaney Cr. Vancouver Island: (55) Stephens Cr., (56) Marble R., (57) Nimpkish R., (58) Tahsish R., (59) Zeballos R., (60) Tahsis R., (61) Sucowa R., (62) Canton R., (63) Conuma R., (64) Burman R., (65) Megin R., (66) Puntledge R., (67) Rosewall Cr., (68) Big Qualicum R., (69) Atleo R., (70) Nahmint R., (71) Thornton Cr., (72) Little Qualicum R., (73) Nanaimo R., (74) Sarita R., (75) Nitinat R., (76) Chemainus R., (77) Cowichan R., (78) Goldstream R.

as early as July in the northern and central areas of British Columbia and as late as January in the southern region (Neave 1966). Age at maturity generally ranges from 3 to 5 yr (Pritchard 1943; Ricker 1980; Beacham 1984), with age 2 and age 6 fish exceptionally rare. Size at maturity ranges from at least 440 to 690 mm postorbital–hypural length, with males more variable in size and body morphology than females (Beacham and Murray 1985a).

Variation in chum salmon in British Columbia is partially a consequence of their diverse spawning times and spawning habitats, and presumably this variation is genetic in origin. Theoretically, variation in life history and morphology is adaptive, and is maintained by selection and homing of chum salmon to their natal streams, yet it remains to be demonstrated empirically that they have specific adaptations to exploit their varying environments.

In 1981 we began examining chum salmon stocks in British Columbia for variation in size and age at maturity and body morphology, and in 1983 we began an examination of comparative developmental biology. In this paper we present evidence which illustrates that chum salmon in British Columbia have variable traits specifically adapted to different environments.

Methods and Materials

Age and Morphology

To examine variation in sex ratios, age, size, and morphology, we surveyed 78 chum salmon stocks and examined over 10 000 salmon. We surveyed chum salmon on the spawning grounds from 12 Fraser River stocks, 9 east coast of Vancouver Island stocks, 15 west coast of Vancouver Island stocks, 12 south coast mainland stocks, 13 central coast mainland stocks, 7 north coast mainland stocks, and 10 stocks from the Queen Charlotte Islands (Fig. 1). Methodology of sample collection on both the spawning grounds and in ocean fisheries has been described by Beacham et al. (1983) and Beacham (1984). Postorbital–hypural length (Vladykov 1962), postorbital–head length (Vladykov 1962), caudal peduncle depth, and

length of the base and height of both the anal and dorsal fins (Hubbs and Lagler 1958) were all recorded on the left side in the field to the nearest millimetre. The number of gillrakers on the left anterior gill arch was recorded, as well as the number of branchiostegal rays on the left side. Scales were collected for age determination following Bilton and Ricker (1965) and LaLanne and Safsten (1969), and the sex was confirmed by internal inspection.

Variation in sex ratios by age and age of maturity in relation to spawning time was examined by chi-square (Sokal and Rohlf 1981). Regional differences and sexual dimorphism in meristic characters were tested by two-way analysis of variance, with region and sex as the indices. There were significantly different allometric regressions ($\log_e$ morphometric character = $\log_e a + b \log_e$ length) between sexes and among stocks within each sex. Morphometric measurements of both males and females were standardized to a postorbital–hypural length of 600 mm by the method outlined by Beacham and Murray (1983):

$$M_t = M_o \left(\frac{\bar{L}}{L_o}\right)^b$$

where M_t = length of standardized morphometric character, M_o = observed character length, $\bar{L}$ = postorbital–hypural length that the characters are standardized to (600 mm), L_o = observed postorbital–hypural length, and b = regression coefficient of $\log_e L$. This allometric regression to a standard size is a preferred method of removing size variation in characters among individuals (Reist 1985).

Size differences in mean length-at-age and in morphometric characters were examined for stocks sampled from "small" or "large" rivers in the seven regions previously outlined. Large rivers were defined as those having a length of at least 8 km and a drainage area in excess of 100 km^2. Variability in mean length-at-age was examined with the analysis of variance model (all effects fixed)

$$Y_{ijklm} = \mu + S_i + A_j + G_k + R_l + AR_{jl} + GR_{kl} + SG_{ik} + e_{ijklm}$$

where Y_{ijklm} = observed mean length-at-age, μ = mean, S_i = effect of sex (i = 1,2), A_j = effect of age (j = 2,6), G_k = effect of region (k = 1,7), R_l = effect of river size (l = 1,2), AR_{jl} = interaction between age and river size, GR_{kl} = interaction between region and river size, SG = interaction between sex and region, and e_{ijklm} = error term for mth observation in subgroup $ijkl$. Variation in mean character size was examined with the analysis of variance model (all effects fixed)

$$Y = \mu + S_i + G_j + GR_{jk} + SG_{ij} + e_{ijkl}$$

with the variables defined as in the previous model.

Developmental Biology

To examine variation in developmental biology, we surveyed 17 stocks and examined 84 separate families. We collected gametes from seven Fraser River, two east coast Vancouver Island, one west coast Vancouver Island, two central coast mainland, three north coast mainland, and two Queen Charlotte Islands stocks. Methodology of gamete collections, egg fertilizations, and incubations have been outlined by Beacham and Murray (1985b, 1986a). Summarized briefly, eggs and sperm were transported to the laboratory on ice. The eggs were fertilized at 8°C and subsequently reared in controlled water temperatures of 2, 4, 8, or 12°C. Eggs of the two stocks which were reared at 2°C were first incubated for 3 d at 8°C. Sperm from a single male fertilized the eggs of a single female producing a single family, and up to five families per stock were examined. The eggs were incubated in vertical stack incubators, with families replicated either two or three times at each incubation temperature. Water temperatures were recorded daily.

Egg diameter (millimetres) and weight (milligrams) for each female were determined from 30 water-hardened eggs preserved for at least 3 mo in 10% formalin. During incubation, dead eggs were removed from each family, stored in Stockard's solution (Rugh 1952), and later inspected to remove unfertilized eggs. Egg survival rates were then calculated based upon the number of eggs initially fertilized. Once hatching began in each family, we recorded the number of newly hatched alevins daily, and within 1 d of 50% hatching we anesthetized and preserved 30 per family in 10% formalin for subsequent determination of alevin length and weight. Fork length was recorded to the nearest 0.1 mm, total weight recorded to the nearest milligram, the yolk separated from the rest of the body and weighed (milligrams), and then tissue weight (milligrams) determined by subtraction. Dead alevins were also removed and counted in order to determine alevin survival rates. The timing of fry emergence (swim-up) for each family was determined by placing the alevins in an emergence trap modified from Godin (1980), where the alevins were classified as newly emergent fry only when they became neutrally buoyant and positively phototactic. When 50% of the fry for a particular family had emerged, all of the family remaining in the incubator was anesthetized and then preserved in 10% formalin, and up to 42 fry were unselectively drawn from the preserved samples and fry length and weight determined as for alevins.

Variation in egg size for the stocks surveyed in 1984 or 1985 was analyzed with the analysis of variance model (all effects random)

$$Y_{ijk} = \mu + S_i + F_{ij} + e_{ijk}$$

where Y_{ijk} = egg diameter or weight, μ = mean, S_i = effect of stock (i = 1,9), F_{ij} = effect of female within stock (j = 1,5), and e_{ijk} = error term for kth observation in subgroup ijk. Heterogeneity in egg and alevin survival rates among stocks and among incubation temperatures surveyed in 1984 was tested by likelihood ratio (G-test) (Sokal and Rohlf 1981). For the analysis of stock and temperature effects on survival for all chum salmon stocks surveyed in British Columbia during 1983–85, we calculated survival rates for each group as proportions and then transformed them to radians with the arcsine square root transformation to make the variance independent of the mean. Variation in survival rate was then analyzed with the analysis of variance model

$$Y_{ijk} = \mu + S_i + T_j + ST_{ij} + e_{ijk}$$

where Y_{ijk} = transformed survival rate, μ = overall mean, S_i = effect of stock (i = 1,17), T_i = effect of temperature (j = 1,3), ST_{ij} = interaction between stock and temperature, and e_{ijk} = error term for kth observation (individual family survival rate) in subgroup ij. Temperature was considered fixed; other effects were considered random.

Variation in alevin and fry length and weight was examined with the model

TABLE 1. Sex ratios of chum salmon of ages 2–6 yr sampled on the spawning grounds on mainland British Columbia (north, central, and south coast), Vancouver Island (east and west coast), the Queen Charlotte Islands, the Fraser River and its tributaries, and from ocean fisheries during 1981–85.

	Age (yr)									
	2		3		4		5		6	
Region	*N*	% male	*N*	% male	*N*	% male	*N*	% male	*N*	% male
Mainland										
North	0	—	84	78.6	833	57.1	84	60.7	2	100.0
Central	0	—	821	60.8	763	54.0	68	69.1	0	—
South	0	—	236	49.2	788	49.1	120	47.5	0	—
Vancouver Island										
East	3	100.0	372	61.0	1172	43.8	76	50.0	0	—
West	3	66.7	924	59.3	940	54.6	29	75.9	1	100.0
Fraser River	0	—	484	53.1	1056	46.4	180	52.8	0	—
Queen Charlotte Is.	0	—	409	63.8	513	54.5	42	81.0	1	0.0
Ocean fisheries	0	—	475	62.4	1227	45.1	53	55.4	0	—
Total	6	83.3	3805	59.7	7292	49.7	652	57.2	4	75.0

$$Y_{ijkl} = \mu + S_i + T_j + ST_{ij} + F_{ik} + FT_{ijk} + e_{ijkl}$$

where Y_{ijkl} = observed length or weight, μ = overall mean, S_i = effect of stock, T_j = effect of temperature, ST_{ij} = interaction between stock and temperature, F_{ik} = effect of family within stock (k = 1,15), FT_{ijk} = interaction between families within stock and temperature, and e_{ijkl} = error term for lth observation in subgroup $ijkl$. Temperature was again considered fixed and other effects random. Satterthwaite's (1946) approximation was necessary to calculate an appropriate mean square to test the effect of stock.

Regional differences in alevin and fry tissue weight were investigated by analysis of covariance with the model

$$Y_{ij} = \mu + R_i + B(W_{ij} - \bar{W}) + e_{ij}$$

where Y_{ij} = tissue weight, μ = mean, R_i = effect of region (i = 1,2) (northern, southern), B = regression coefficient of tissue weight on mean stock egg size, W_{ij} = mean egg weight by stock (j = 1,7 for northern region and 1,10 for southern region), $\bar{W}$ = overall mean egg weight, and e_{ij} = error term for jth observation in subgroup i. Temperatures were considered separately in the analysis.

Results

Age and Morphology

Sex ratios

Sex ratios of mature chum salmon varied with age (Table 1). With samples from the spawning grounds and ocean fisheries pooled, it was evident that males returned at higher frequencies than did females at 3 yr ($\chi^2 = 71.8$ $P < 0.01$) and 5 yr of age ($\chi^2 = 6.8$, $P < 0.01$), but the differences were not significant at either 2 yr ($\chi^2 = 2.7$, $P > 0.05$) or 6 yr of age ($\chi^2 = 1.0$, $P > 0.05$). At 4 yr, the main age of maturity, males were less abundant than females ($\chi^2 = 0.2$, $P > 0.05$), but at younger and older ages of maturity, males predominated.

Age of maturity

There were regional and spawning timing differences in age at maturity. Age at maturity of chum salmon in British Columbia ranged from 2 to 6 yr, with 3 and 4 yr being the dominant ages of maturity (Table 2). Timing of spawning had a marked effect on age at maturity. Within an area, early-spawning stocks had higher proportions of older chum salmon than did late-spawning ones, with mean age of the spawners declining as the spawning season progressed. Late-spawning stocks had greater proportions of age 3 spawners than did early-spawning stocks in the north coast area ($\chi^2 = 4.18$, $P < 0.05$), the central coast (August versus September–November, $\chi^2 = 328.1$, $P < 0.01$), the Queen Charlotte Islands ($\chi^2 = 0.32$, $P > 0.05$), the south coast (September and October versus November and December, $\chi^2 = 5.34$, $P < 0.05$), the Fraser River (October–November versus December $\chi^2 = 73.45$, $P < 0.01$), and the west coast ($\chi^2 = 0.08$, $P > 0.05$) of Vancouver Island. The proportion of age 5 spawners declined as the proportion of age 3 increased.

Meristics

No sexual dimorphism in mean number of gillrakers or branchiostegal rays was detected in our survey of chum salmon in British Columbia (both $P > 0.05$). There were regional differences in gillraker and branchiostegal ray number, with northern stocks tending to have higher mean counts in these meristic characters than southern stocks (Table 3). Chum salmon in an area characterized by a lower number of gillrakers also had a lower number of branchiostegal rays ($r = 0.86$, $N = 7$, $P < 0.05$).

Morphometry

In British Columbia, chum salmon spawn in a wide variety of habitats, ranging from small creeks to the mainstems of large rivers, and we investigated whether there were any consistent morphological differences among chum salmon correlated with river size. For our analysis, we compared chum salmon from 78 rivers classified as either "small" or "large" in the seven geographic areas as outlined in Table 4. The analysis indicated that males were larger than females ($F_{1,9978} = 453.1$, $P < 0.01$). There was regional differentiation in postorbital–hypural length ($F_{6,9978} = 66.9$, $P < 0.01$), with chum salmon from the Queen Charlotte Islands and the west coast of Vancouver Island being the shortest in all the areas surveyed, and

TABLE 2. Percentage of all chum salmon returning at ages 2–6 yr and mean age of return for chum salmon stocks sampled on the spawning grounds in northern and southern British Columbia during 1981–85.

Region	Month	N	Age (yr) 2	3	4	5	6	Mean age (yr)
Northern British Columbia								
North coast	August	903	0.0	9.0	81.6	9.2	0.2	4.01
	September	100	0.0	3.0	96.0	1.0	0.0	3.98
Central coast	August	677	0.0	22.9	68.2	8.9	0.0	3.86
	September	875	0.0	66.2	32.9	0.8	0.0	3.34
	November	100	0.0	86.0	13.0	1.0	0.0	3.15
Queen Charlotte Is.	September	466	0.0	41.4	55.0	3.4	0.2	3.62
	October	500	0.0	43.2	51.6	5.2	0.0	3.57
Southern British Columbia								
South coast	September	100	0.0	1.0	54.0	45.0	0.0	4.44
	October	308	0.0	22.1	67.9	10.1	0.0	3.88
	November	435	0.0	27.8	68.0	4.1	0.0	3.76
	December	301	0.0	15.3	76.0	8.6	0.0	3.93
Fraser River	October	300	0.0	9.3	54.7	36.0	0.0	4.27
	November	1000	0.0	29.7	64.9	5.4	0.0	3.70
	December	420	0.0	37.9	57.9	4.3	0.0	3.67
Vancouver Island								
East coast	October	200	0.0	3.0	90.0	7.0	0.0	4.04
	November	892	0.1	19.7	74.0	6.1	0.0	3.86
	December	532	0.4	35.7	62.4	1.5	0.0	3.65
West coast	October	1497	0.2	48.6	49.4	1.8	0.1	3.53
	November	400	0.0	49.3	50.2	0.5	0.0	3.51

TABLE 3. Mean number of gillrakers on left anterior gill arch and mean number of branchiostegal rays of left side for chum salmon sampled in British Columbia during 1981–85. Standard errors of mean are given in parentheses.

Region	N	Gillrakers	Branchiostegal rays
Northern British Columbia			
North coast	703	22.90 (0.05)	13.44 (0.03)
Central coast	1452	23.20 (0.03)	13.70 (0.04)
Queen Charlotte Is.	966	23.23 (0.04)	13.49 (0.03)
Southern British Columbia			
South coast	1144	22.00 (0.04)	13.28 (0.03)
Fraser River	1720	22.23 (0.03)	13.35 (0.02)
Vancouver Island			
East coast	1624	21.98 (0.03)	12.98 (0.02)
West coast	1597	23.09 (0.03)	13.75 (0.02)

within an area, chum salmon spawning in large rivers tending to be longer than those spawning in small rivers when the same ages were compared ($F_{1,9978} = 6.53$, $P < 0.05$) (Table 5). Chum salmon from large rivers clearly have higher growth rates in the ocean than do chum salmon from small rivers.

We investigated whether there was differentiation in the relative sizes of six morphometric characters, after the sizes of the characters had been standardized to an individual of 600 mm postorbital–hypural length by allometric regression. As expected, there was sexual dimorphism in all of the six characters examined, with males having a larger postorbital head length than females (96.0 versus 87.8 mm, $F_{1,8886} = 5333.6$, $P < 0.01$), a thicker caudal peduncle (50.3 versus 48.3 mm, $F = 376.7$, $P < 0.01$), a longer dorsal fin base length (78.0 versus 70.8 mm, $F = 2584.5$, $P < 0.01$) and dorsal fin height (106.0 versus 97.3 mm, $F = 1769.9$, $P < 0.01$), but a shorter base length of the anal fin (82.0 versus 82.7 mm, $F = 19.42$, $P < 0.01$), as well as anal fin height (69.8 versus 70.0 mm, $F = 14.96$, $P < 0.01$) (Table 6). There was also differentiation in all morphometric characters among the geographic areas examined (all $P < 0.01$) (Table 6). There were also clear differences in relative sizes of the six morphometric characters surveyed between chum salmon spawning in large and small rivers. Chum salmon from large rivers had a longer postorbital head length (92.3 versus 92.2 mm, $F_{1,8886} = 42.8$, $P < 0.01$), a thicker caudal peduncle (49.5 versus 48.9 mm, $F = 262.3$, $P < 0.01$), a longer base length (82.4 versus 82.2 mm, $F = 38.7$, $P < 0.01$) and height (70.5 versus 68.7 mm, $F = 113.3$, $P < 0.01$) of the anal fin, and a longer base length (74.9 versus 74.8 mm, $F = 12.9$, $P < 0.01$) and height (102.2 versus 102.1 mm, $F = 10.2$, $P < 0.01$) of the dorsal fin when compared with chum salmon from small rivers. In summary, males had larger heads, thicker caudal peduncles, and larger dorsal fins than females, but females had larger anal fins than males. Chum salmon from large rivers had larger heads, thicker caudal peduncles, and larger anal and dorsal fins than chum salmon from small rivers.

Developmental Biology

Egg size

In 1984 and 1985, we surveyed stocks spawning from August through January (Table 7). When we combined the data on egg size and spawning time of the chum salmon stocks surveyed in 1983 (Beacham and Murray 1985b, 1986a) with the data from the stocks surveyed in 1984 and 1985, there were clear regional and seasonal trends in egg size. In both northern and southern British Columbia, egg size declines as the spawning season progresses (Table 8). Spawning begins earlier in the northern region than in the southern one, so that in October and November when spawning is occurring in both the northern and southern regions, egg size is larger in the southern region. The

TABLE 4. Classification of rivers in seven geographic regions in British Columbia. Large rivers were those with a drainage area in excess of 100 km^2 and a length in excess of 8 km.

Region	River size	Rivers
Northern British Columbia		
North coast	Large	Toon, Khutzeymateen, Kitsault, Kshwan, Stagoo, Nass, Ecstall
Central coast	Small	Green, Cascade, Elcho
	Large	Bella Coola, Kemano, Kimsquit, Clyak, Kitimat, Mussel, Neekas, Kainet, Nekite, Wannock
Queen Charlotte Is.	Small	Tasu, Security, Stanley, Deena, Lagins, Pallant, Lagoon, Awun, Salmon
	Large	Ain
Southern British Columbia		
South coast	Small	Sliammon, Okeover, Saltery
	Large	Orford, Homathko, Southgate, Toba, Squamish, Cheakamus, Mamquam, Tzoonie, Indian
Fraser River	Small	Blaney, Squakum, Weaver, Inch, Chilqua
	Large	Vedder, Stave, mainstem Fraser, Wahleach, Chehalis, Harrison, Alouette
Vancouver Island		
East coast	Small	Goldstream, Rosewall
	Large	Cowichan, Chemainus, Nanaimo, Little Qualicum, Big Qualicum, Puntledge, Nimpkish
West coast	Small	Thornton, Atleo, Sucwoa, Canton
	Large	Nitinat, Sarita, Marble, Conuma, Tashsish, Nahmint, Tahsis, Zeballos, Megin, Stephens, Burman

TABLE 5. Mean postorbital–hypural length-at-age (mm) and overall mean length for chum salmon from large and small rivers in seven regions in British Columbia sampled during 1981–85. Large rivers were those greater than 8 km in length and having a drainage area of greater than 100 km^2. Sample sizes are given in parentheses.

		Male				Female			
		Age (yr)				Age (yr)			
Region	River size	3	4	5	Mean	3	4	5	Mean
Northern British Columbia									
North coast	Large	518(66)	605(476)	620(51)	597(595)	505(18)	575(357)	588(33)	573(408)
Central coast	Small	492(143)	538(48)	— (0)	504(191)	490(86)	531(23)	— (0)	498(109)
	Large	567(356)	613(380)	668(47)	595(783)	535(236)	590(312)	632(21)	569(569)
Queen Charlotte Islands	Small	528(225)	569(295)	603(24)	553(544)	522(138)	562(177)	600(6)	546(322)
	Large	529(36)	584(36)	605(10)	563(82)	515(11)	558(5)	612(2)	538(18)
Southern British Columbia									
South coast	Small	540(50)	580(90)	588(7)	567(147)	542(49)	575(73)	589(4)	563(126)
	Large	573(66)	618(344)	626(50)	612(460)	560(71)	604(281)	602(59)	596(411)
Fraser River	Small	543(128)	575(123)	616(25)	564(276)	531(115)	572(99)	607(35)	558(249)
	Large	560(129)	598(368)	608(70)	590(567)	541(112)	581(466)	603(50)	576(628)
Vancouver Is.									
East coast	Small	548(37)	581(70)	599(4)	569(112)	549(19)	565(49)	625(4)	564(72)
	Large	557(190)	602(443)	626(34)	590(670)	547(126)	584(610)	613(34)	579(770)
West coast	Small	531(184)	573(101)	— (0)	546(285)	527(116)	558(99)	— (0)	541(215)
	Large	540(364)	583(412)	595(22)	564(800)	532(260)	563(328)	595(7)	550(597)

seasonal decline in egg size is also coincident with a seasonal decline in mean age of the spawners (Table 2), with progressively younger fish laying progressively smaller eggs. There were significant differences in mean egg diameter ($F_{8,28} = 6.20$, $P < 0.01$) and egg weight ($F = 6.46$, $P < 0.01$) among stocks surveyed during 1984–85, where variation among stocks in egg diameter and egg weight accounted for 39 and 54% of the total variance, respectively. Significant differences were also observed among females within stocks in both egg diameter ($F_{28,1070} = 27.89$, $P < 0.01$) and weight ($F = 193.51$, $P < 0.01$), accounting for 29 and 40% of the total variance, respectively. The stock and female components accounted for more variation in egg weight (94%) than in egg diameter (58%).

Survival rates

During 1984–85, we compared developmental biology of chum salmon stocks spawning from August through January (Table 7). Highest embryo survival rates for most stocks were recorded at an incubation temperature of 8°C, while the lowest were recorded at 2°C (Table 9). Differences in survival rates among incubation temperatures were significant ($G = 4524$, $P < 0.01$). Embryo survival rates were usually over 90% at incubation temperatures of 4, 8, and 12°C. At 2°C, survival

TABLE 6. Mean measurements (mm) for chum salmon sampled in small and large rivers in sev
to a postorbital–hypural length of 600 mm. Large rivers were those greater than 8 km in length

Character	North coast	Central coast		Queen Charlotte Islands		
	Large rivers	Small rivers	Large rivers	Small rivers	Large rivers	S r
Male						
Head	95.5(0.3)	92.9(0.5)	95.3(0.3)	98.6(0.2)	95.4(0.4)	93
Caudal penduncle	51.4(0.2)	48.0(0.3)	52.3(0.2)	52.4(0.1)	53.1(0.4)	46
Anal fin base	83.2(0.5)	80.6(0.7)	81.5(0.7)	85.6(0.4)	85.7(0.5)	78
Anal fin height	70.8(0.3)	61.3(0.5)	71.6(0.3)	69.1(0.3)	69.0(0.8)	69
Dorsal fin base	80.6(0.3)	77.7(0.6)	80.5(0.4)	79.4(0.2)	79.7(0.4)	75
Dorsal fin height	107.5(0.4)	105.0(0.6)	107.7(0.4)	106.6(0.4)	108.1(0.6)	105
Sample size	401	191	544	544	82	147
Female						
Head	87.5(0.3)	84.0(0.4)	87.6(0.3)	88.8(0.2)	88.2(0.7)	86
Caudal peduncle	50.3(0.3)	46.7(0.3)	50.0(0.2)	50.6(0.2)	52.8(0.6)	45
Anal fin base	85.4(0.6)	74.4(0.6)	85.1(0.6)	84.8(0.7)	86.6(1.1)	79
Anal fin height	71.6(0.4)	59.7(0.6)	68.8(0.4)	70.8(0.4)	69.8(1.4)	68
Dorsal fin base	74.1(0.4)	71.9(0.5)	73.9(0.3)	71.3(0.2)	72.9(0.8)	67
Dorsal fin height	101.3(0.5)	92.6(0.8)	100.2(0.4)	98.4(0.5)	103.1(1.5)	97
Sample size	302	109	408	322	18	126

rs in seven regions of British Columbia during 1981–85. Measurements for each individual were standardized in length and having a drainage area of greater than 100 km^2. Standard errors are given in parentheses.

ds	South coast		Fraser River		Vancouver Island			
					East coast		West coast	
	Small rivers	Large rivers	Small rivers	Large rivers	Small rivers	Large rivers	Small rivers	Large rivers
.4)	93.7(0.4)	94.9(0.2)	96.2(0.3)	98.0(0.2)	94.3(0.4)	95.4(0.2)	95.8(0.3)	97.3(0.2)
.4)	46.7(0.3)	49.1(0.2)	48.5(0.2)	50.2(0.2)	47.5(0.5)	49.0(0.1)	48.8(0.4)	50.9(0.2)
.5)	78.0(0.5)	79.8(0.3)	80.3(0.4)	82.1(0.3)	78.2(0.2)	79.0(0.2)	84.2(0.4)	85.2(0.3)
.8)	69.0(0.6)	70.7(0.3)	70.9(0.3)	72.4(0.2)	68.8(0.5)	69.1(0.2)	66.6(0.5)	70.3(0.3)
.4)	75.2(0.4)	76.3(0.3)	76.5(0.3)	77.2(0.2)	77.1(0.6)	74.7(0.2)	77.9(0.5)	80.0(0.3)
.6)	105.0(0.6)	104.9(0.5)	105.0(0.4)	105.9(0.3)	107.6(0.7)	105.6(0.4)	101.7(0.7)	104.9(0.4)
	147	460	276	567	112	670	232	636
.7)	86.7(0.4)	87.9(0.2)	88.9(0.3)	89.4(0.2)	88.1(0.4)	86.8(0.2)	86.0(0.3)	88.4(0.2)
.6)	45.9(0.3)	47.5(0.2)	46.4(0.3)	48.5(0.2)	46.2(0.4)	47.7(0.2)	47.5(0.2)	48.2(0.2)
.1)	79.1(0.5)	79.5(0.3)	81.3(0.6)	83.1(0.3)	79.8(0.8)	80.9(0.2)	84.2(0.6)	86.2(0.3)
.4)	68.8(0.5)	70.8(0.4)	72.2(0.3)	72.2(0.2)	68.8(0.6)	69.3(0.2)	67.4(0.5)	68.5(0.3)
.8)	67.6(0.5)	69.6(0.3)	69.4(0.3)	70.7(0.2)	67.2(0.6)	68.5(0.2)	71.4(0.4)	71.5(0.2)
.5)	97.3(0.5)	96.5(0.5)	97.2(0.4)	97.6(0.3)	95.2(0.9)	96.9(0.3)	94.0(0.6)	96.0(0.4)
	126	411	249	628	72	770	168	461

TABLE 7. Egg fertilization dates in 1984 or 1985 and surface water temperatures for chum salmon stocks sampled in British Columbia.

Region	Stock	Date	Temperature (°C)
Central coast	Bella Coola	August 1	11.5
North coast	Khutzeymateen	August 17	10.0
North coast	Kshwan	August 22	9.0
North coast	Stagoo	August 22	9.0
Queen Charlotte Islands	Lagins	September 17	10.0
Queen Charlotte Islands	Pallant	October 11	9.5
Vancouver Island	Chemainus early	October 31	8.0
Central coast	Wannock	November 10	7.0
Vancouver Island	Chemainus late	January 10	3.5

TABLE 8. Mean egg weight and diameter by monthly periods for 17 chum salmon stocks spawning in either northern or southern British Columbia. Eggs were water-hardened before sampling and preserved in 10% formalin. Thirty eggs were weighed for each female. Standard deviations are given in parentheses.

	Northern			Southern		
Period	*N*	Weight (mg)	Diameter (mm)	*N*	Weight (mg)	Diameter (mm)
August	450	316.9(32.7)	8.59(0.36)	0	—	—
September	60	283.1(41.5)	8.41(0.44)	0	—	—
October	150	265.2(20.9)	8.21(0.32)	1260	293.3(48.2)	8.44(0.41)
November	150	246.2(18.2)	7.98(0.31)	150	289.1(37.0)	8.23(0.30)
December	0	—	—	150	263.2(12.3)	7.94(0.35)
January	0	—	—	150	251.0(28.9)	7.89(0.28)

rates were lower than at either 4°C ($G = 2980$, $P < 0.01$), 8°C ($G = 3713$, $P < 0.01$), or 12°C ($G = 3531$, $P < 0.01$). At 4°C, they were lower than at either 8°C ($G = 75$, $P < 0.01$) or 12°C ($G = 55$, $P < 0.01$). At 8°C, they were higher than at 12°C ($G = 4.8$, $P < 0.05$). Incubation temperature had a marked effect on subsequent embryo survival.

Survival rates of embryos differed among stocks within incubation temperatures at 4°C ($G = 371$, $P < 0.01$), 8°C ($G = 295$, $P < 0.01$), and at 12°C ($G = 249$, $P < 0.01$), but not at 2°C ($G = 0.01$, $P > 0.10$). However, only two stocks were compared at a 2°C incubation temperature. Highest embryo survival rates at 4°C were recorded in the Wannock River stock, the latest-spawning stock surveyed in northern British Columbia. The highest survival rates recorded at 12°C were found in the early-spawning Chemainus River stock, an early-spawning stock in southern British Columbia (Table 9). Within a stock, there were marked differences in embryo survival rates among families (Fig. 2). These differences were greatest at 2°C, where embryo survival rates ranged from 14 to 90% for the four Khutzeymateen River families. Similar differences were also recorded for the five Bella Coola River families at 2°C. Within a stock, apparently families were not all equally adapted to survive in similar environments.

As with embryos, the highest alevin survival rates were recorded at an incubation temperature of 8°C, while the lowest were recorded at 2°C (Table 9), with the differences in survival rates among temperatures highly significant ($G = 335$, $P < 0.01$). Chum salmon alevins incubated at 2°C had significantly lower survival rates than did those at other temperatures examined (4°C, $G = 50$, $P < 0.01$; 8°C, $G = 212$, $P < 0.01$; 12°C, $G = 44$, $P < 0.01$). Unlike the embryos, chum salmon alevins incubated at 4 and 12°C survived equally well ($G = 0.7$, $P > 0.10$), but the alevins incubated at 8°C had higher survival rates than did those at either 4°C ($G = 178$, $P < 0.01$) or 12°C ($G = 203$, $P < 0.01$). Very low incubation temperatures reduce the survival of both embryos and alevins.

Alevin survival differed among stocks within each incubation temperature (2°C, $G = 24$, $P < 0.01$; 4°C, $G = 663$, $P < 0.01$; 8°C, $G = 116$, $P < 0.01$; 12°C, $G = 449$, $P < 0.01$). However, alevin survival rates were usually above 95% for each stock in each temperature regime ≥ 4°C, indicating that incubation temperature had a greater effect on embryo than on alevin survival. As with embryos, there were marked differences in alevin survival rates among families within stocks, with the difference most apparent at the extreme incubation temperatures (Fig. 2).

We examined trends in embryo survival rates by combining data from the seven Fraser River chum salmon stocks (Beacham and Murray 1986a) and from the Nitinat River stock (Beacham and Murray 1985b) with those reported in the present study. There were significant differences in embryo survival rates among the 17 stocks examined ($F_{16,32} = 8.64$, $P < 0.01$) and among the three incubation temperatures (4, 8, and 12°C) ($F_{2,32} = 13.63$, $P < 0.01$). The trends in embryo survival with respect to incubation temperature were similar in all stocks ($F_{32,201} = 1.12$, $P > 0.10$). For all stocks combined, highest embryo survival rates were recorded at 8°C and the lowest at 4°C, the same result as was found for the stocks surveyed in 1983.

The 17 chum salmon stocks surveyed in British Columbia covered a wide geographic range and diverse spawning times. We grouped the embryo survival rates of those stocks spawning before November when surface water temperatures were ≥8°C separately from those spawning later when surface water temperatures were ≤7°C. We expected the embryos from later-spawning stocks to be more resistant to colder water temperatures than those from early-spawning stocks. At 4°C, embryos from late-spawning stocks had higher survival rates than

TABLE 9. Survival rates of fertilized eggs and alevins for nine stocks of chum salm
and 12°C. Time of 50% hatching of the alevins and 50% emergence of the fry are
regime for each stock is also recorded. *N* is the number of fertilized eggs (for e
tions of mean temperatures and 50% hatching and emergence times are given in

			Egg		
			Survival rate		
Region	Stock	Temperature (°C)	*N*	Fetilization to hatching	Time to hatchin
Central coast	Bella Coola	2.2(0.44)	2728	0.595	186.8(
		4.1(1.20)	2844	0.974	124.5(
		8.1(0.41)	2674	0.982	69.3(
		12.0(0.60)	2788	0.988	46.6(
North coast	Khutzeymateen	2.2(0.42)	615	0.592	185.3(
		4.1(0.92)	1087	0.890	122.5(
		7.9(0.36)	1108	0.924	69.3(
		12.0(0.39)	888	0.912	45.0(
North coast	Kshwan	4.1(0.67)	1516	0.920	121.7(
		8.0(0.32)	1433	0.946	67.9(
		12.0(0.35)	1520	0.939	45.9(
North coast	Stagoo	4.1(0.67)	587	0.985	121.0(
		8.0(0.32)	536	0.998	67.6(
		12.0(0.35)	459	0.989	45.5(
Queen Charlotte Islands	Lagins	4.1(0.39)	426	0.988	140.6(
		8.0(0.35)	454	0.991	78.3(
		12.0(0.33)	484	0.975	53.2(
Queen Charlotte Islands	Pallant	4.1(0.39)	1932	0.977	138.0(
		8.1(0.39)	2068	0.993	75.9(
		12.1(0.38)	2140	0.982	50.8(
Vancouver Island	Chemainus (early)	4.1(0.36)	2415	0.983	116.9(
		8.1(0.38)	2335	0.997	63.8(
		12.1(0.46)	2461	0.995	43.3(
Central coast	Wannock	4.1(0.38)	2397	0.990	125.1(
		8.1(0.37)	2313	0.995	67.7(
		12.0(0.39)	2113	0.985	46.1(
Vancouver Island	Chemainus (late)	4.1(0.45)	2089	0.930	114.3(
		8.0(0.30)	2431	0.977	65.9(
		12.0(0.35)	2371	0.978	44.3(

hum salmon sampled in 1984 or 1985 and incubated at controlled temperatures of 2, 4, 8, ne fry are also indicated. Mean temperature observed under each controlled temperature gs (for egg survival rates) or alevins hatching (for alevin survival rates). Standard devia- given in parentheses.

		Alevin			
			Survival rate		
Time to 50% hatching (d)	Temperature (°C)	*N*	Hatching to emergence	Fertilization to emergence	Time to 50% emergence (d)
186.8(2.5)	2.2(0.42)	1622	0.909	0.541	327.6(6.2)
124.5(1.4)	4.0(1.52)	2771	0.946	0.921	204.1(2.9)
69.3(0.7)	8.0(0.41)	2627	0.993	0.975	132.3(3.7)
46.6(0.5)	12.1(0.78)	2754	0.996	0.984	99.4(6.4)
185.3(3.7)	2.1(0.27)	364	0.978	0.579	314.5(5.8)
122.5(1.3)	4.1(0.75)	967	0.994	0.884	201.2(1.9)
69.3(0.5)	8.0(0.40)	1024	0.995	0.920	121.7(11.2)
45.0(0.3)	12.0(0.34)	810	0.949	0.866	101.8(8.9)
121.7(1.6)	4.1(0.57)	1395	0.920	0.847	203.4(3.1)
67.9(1.0)	8.1(0.37)	1356	0.992	0.939	117.0(2.6)
45.9(0.7)	12.0(0.35)	1427	0.862	0.809	97.6(3.3)
121.0(0.2)	4.1(0.57)	578	0.984	0.969	204.4(2.0)
67.6(0.6)	8.1(0.37)	535	0.992	0.991	111.5(0.7)
45.5(0.8)	12.0(0.35)	454	0.993	0.983	94.1(4.4)
140.6(0.2)	4.1(0.40)	421	0.998	0.986	214.0(3.5)
78.3(1.3)	8.0(0.36)	450	1.000	0.991	122.4(1.9)
53.2(0.4)	12.0(0.38)	472	0.951	0.928	87.5(0.7)
138.0(2.1)	4.1(0.42)	1888	0.996	0.973	209.6(1.3)
75.9(0.3)	8.1(0.37)	2054	0.994	0.987	115.3(4.1)
50.8(1.0)	12.0(0.37)	2102	0.970	0.953	86.9(1.2)
116.9(1.0)	4.1(0.41)	2375	0.992	0.976	185.7(2.8)
63.8(0.4)	8.1(0.36)	2327	0.978	0.975	103.5(0.8)
43.3(0.3)	12.0(0.42)	2449	0.936	0.931	78.5(2.7)
125.1(2.5)	4.1(0.40)	2374	0.987	0.977	190.8(3.1)
67.7(0.7)	8.1(0.32)	2302	0.963	0.958	116.1(2.7)
46.1(0.4)	12.0(0.40)	2081	0.960	0.946	78.4(2.7)
114.3(2.3)	4.1(0.39)	1942	0.870	0.808	180.0(1.0)
65.9(0.9)	8.0(0.33)	2334	0.982	0.960	101.6(0.9)
44.3(0.4)	12.1(0.42)	2319	0.973	0.952	71.9(1.1)

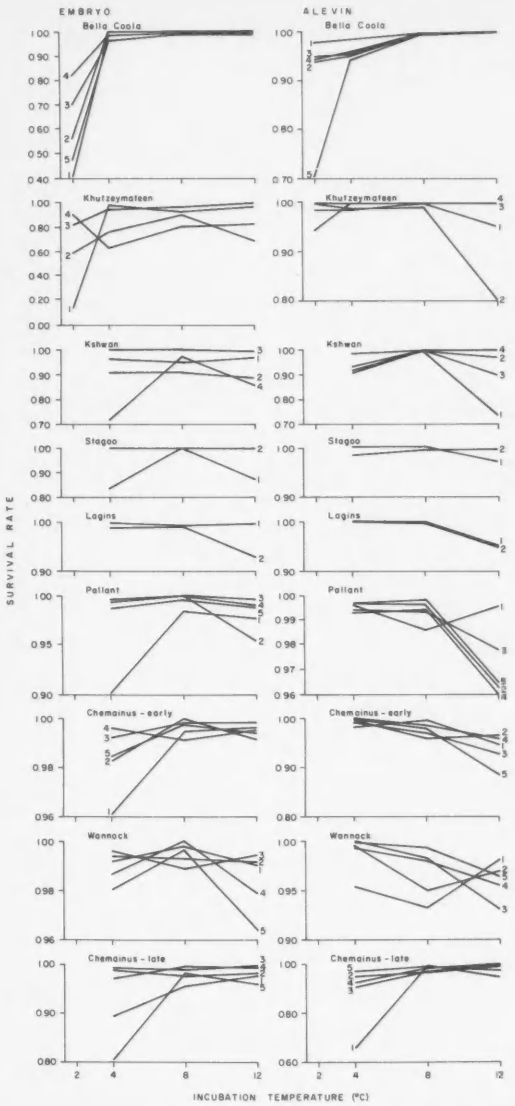

FIG. 2. Survival rates of embryos from fertilization to hatching and of alevins from hatching to emergence for 37 families from nine stocks of chum salmon. Families within stocks are numbered from 1 to 5.

did those from early-spawning ones ($G = 80.6$, $P < 0.01$) (Table 10). At 8°C, the late-spawning stocks had lower embryo survival rates than did the early-spawning ones ($G = 86.5$, $P < 0.01$). Unexpectedly, however, the late-spawning stocks also had higher embryo survival at 12°C than did the early-spawning ones ($G = 142.0$, $P < 0.01$). Chum salmon embryo survival rates at controlled temperatures clearly differ among early- and late-spawning stocks.

We compared alevin survival rates for the 17 stocks surveyed and found no significant difference among stocks ($F_{16,32} = 0.56$, $P > 0.10$) but a clear difference among temperatures ($F_{2,32} = 12.54$, $P < 0.01$), with alevins at 12°C having lower survival rates than those at either 8 or 4°C. Unlike embryos, there was a significant interaction between stock and incubation temperature ($F_{32,201} = 12.05$, $P < 0.01$), which indicates that trends in alevin survival rates with respect to temperature were not similar in all stocks. Some stocks had higher alevin survival rates at 4 than at 12°C (Khutzeymateen, Kshwan, Lagins, Pallant, Wannock, early Chemanus), whereas others have higher alevin survival rates at 12 than at 4°C (Bella Coola, Stagoo, late Chemainus) (Table 9; Fig. 2). No trends in alevin survival rates with respect to spawning time or location were apparent for the 17 stocks surveyed.

Hatching and emergence time

There was significant regional variation in alevin hatching time of chum salmon stocks in British Columbia, with alevins in the Queen Charlotte Islands stocks hatching 15–25 d later at a 4°C incubation temperature and 8–10 d later at 12°C than those in other stocks (Table 9; Fig. 3). Spawning time had no marked effect on alevin hatching time, with alevins from the early- and late-spawning Chemainus River stocks, separated in spawning time by approximately 2.5 mo, hatching at approximately the same time under the same incubation temperatures. Hatching times of alevins from both Chemainus River stocks were the fastest of those stocks surveyed in British Columbia (Table 9). Except for the Queen Charlotte Island stocks, British Columbia chum salmon stocks have similar hatching times at the same incubation temperatures (Fig. 3).

In contrast with alevin hatching times, there were clear differences among stocks in timing of fry emergence or swim-up (Table 9; Fig. 4). Fry from early-spawning stocks, consisting of older fish producing larger eggs, took longer to emerge than did fry from late-spawning stocks, consisting of younger fish with smaller eggs (Fig. 4). Southern stocks, spawning later than those in northern British Columbia, produce fry emerging considerably faster than those in northern British Columbia (Fig. 4). Although fry from the Queen Charlotte Islands stocks took the longest to hatch at 4, 8, and 12°C, they emerged earlier than did fry from other northern stocks (Table 9; Fig. 4).

Alevin size

Size of alevins at hatching for the stocks surveyed in 1984 was variable both among stocks at a similar incubation temperature and among temperatures within a stock (Table 11). Alevins hatching at 8°C were the longest (22.9 mm), those at 4°C slightly shorter (22.5 mm), and those at 12°C (22.2 mm) and 2°C (20.6 mm) the shortest ($F_{3,17} = 9.00$, $P < 0.01$). Although alevins hatching from stocks incubated at 2°C were the shortest, only alevins incubated at 8°C had heavier non-yolk (tissue) body weights than those incubated at 2°C.

We compared trends in alevin size for all 17 stocks surveyed at incubation temperatures of 4, 8, and 12°C, with replicates for each family combined. As indicated for just the nine stocks surveyed in 1984, alevin length clearly differed among incubation temperatures ($F_{2,32} = 6.04$, $P < 0.01$), with the longest alevins generally produced at 8°C (23.2 mm), those at 4°C intermediate in length (22.7 mm), and those at 12°C being the shortest (22.4 mm). Alevins hatching at 8°C also had the heaviest body weight (288 mg), with body weight declining at 12°C (283 mg) and 4°C (273 mg) incubation temperatures ($F = 8.04$, $P < 0.01$). On average, alevin tissue weights were the greatest at 8°C (118 mg), intermediate at 12°C (110 mg), and the least at 4°C (107 mg) ($F = 6.54$, $P < 0.01$). Incubation temperature had a marked effect on alevin length, weight, and the conversion of egg yolk to body tissue, with the longest and heaviest alevins produced under an 8°C incubation regime.

TABLE 10. Embryo survival rates for 17 chum salmon stocks spawning from August through October and November through January in British Columbia and incubated at controlled water temperatures of 4, 8, and 12°C. Surface water temperature at spawning time for the August through October group was ≥8°C, whereas that for the November through January group was ≤7°C. Sample sizes are given in parentheses.

	Incubation temperature (°C)		
Group	4	8	12
August–October	0.897(35 796)	0.972(32 773)	0.881(34 200)
November–January	0.935(10 681)	0.953(10 794)	0.912(10 250)

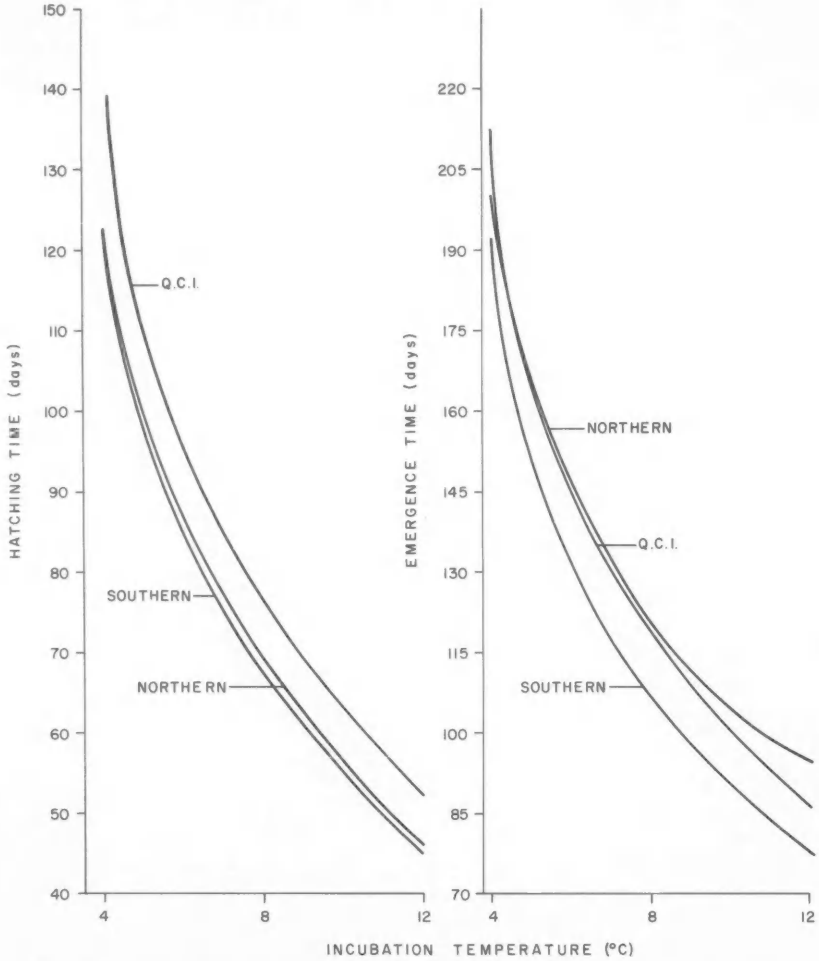

FIG. 3. Mean time of alevin hatching and fry emergence versus incubation temperature for chum salmon stocks from the Queen Charlotte Islands and northern and southern British Columbia. All stocks sampled within each area were pooled.

In contrast, alevin yolk weight at hatching declined with declining incubation temperature. Alevin yolk weights at hatching also varied significantly among incubation temperatures ($F = 9.75$, $P < 0.01$), with alevins hatching at 12°C having the greatest yolk weight (174 mg), those at 8°C intermediate in weight (169 mg), and those at 4°C having the least yolk (167 mg).

Stock differences in mean alevin length ($F_{16,46} = 2.51$, $P < 0.01$)., total weight ($F = 2.88$, $P < 0.01$), yolk weight ($F = 4.66$), and tissue weight ($F = 2.41$, $P < 0.01$) were also

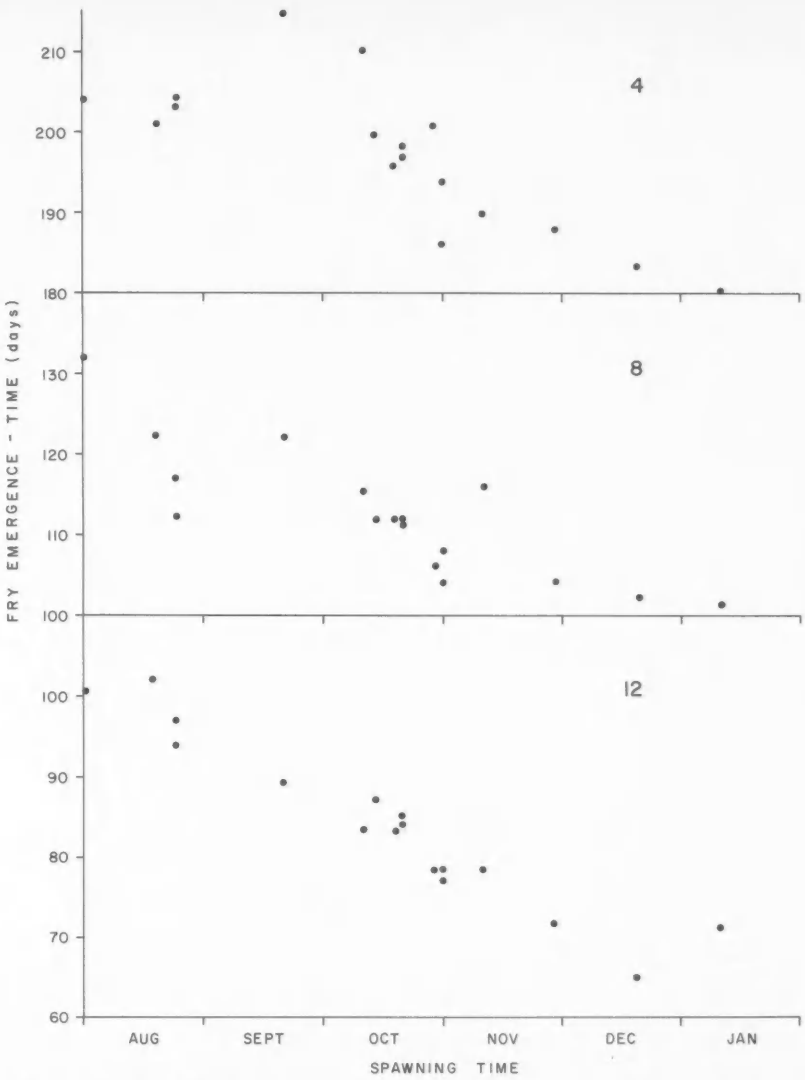

FIG. 4. Mean time of fry emergence versus spawning time for 17 stocks of British Columbia chum salmon incubated at constant temperatures of 4, 8, and 12°C.

observed, but these differences were largely a result of differences in mean egg size among stocks. Longer, heavier alevins were produced by stocks with larger eggs. Significant variation among females within stocks was observed for all alevin size parameters investigated (all $P < 0.01$) (Fig. 5), but this variation was again a result of differences in female egg size within stocks.

If stocks are adapted to different environments with respect to alevin size, then there should be an interaction between stock and incubation temperature, which would be indicative of different trends in alevin size among stocks with respect to incubation temperature. Significant interactions were observed between stock and incubation temperature for alevin fork length ($F_{32,134} = 10.38$, $P < 0.01$), total weight ($F = 6.64$, $P < 0.01$), yolk weight ($F = 2.89$, $P < 0.01$), and tissue weight ($F = 7.53$, $P < 0.01$). Interactions between stocks and temperature for alevin fork length and tissue weight are illustrated in Fig. 6 for three chum salmon stocks: Jones Creek (a tributary to the Fraser River), Pallant Creek (Queen Charlotte Islands), and Nitinat River (west coast of Vancouver Island). Tissue weight of Nitinat River alevins increased at 12°C, unlike the two other stocks illustrated. Tissue weight of Pallant Creek alevins was greatest at 8°C and least at 12°C (Table 11), in direct contrast with the trend in the Nitinat River stock. There are clear differences among stocks in response to incubation temperature for alevin size parameters.

Interactions were also observed among families within stocks and incubation temperature for all alevin size parameters (all $P < 0.01$) (Fig. 5). Families within stocks react differently to changing environments, illustrating that families within

TABLE 11. Egg weights and diameter, fork lengths, total weights, yolk weights, and tissue w
atures. *N* is number of alevins or fry measured and weighed for all families combined in

Stock	Egg weight (mg) and diameter (mm)	Temperature (°C)	Alevin *N*	Fork length (mm)	Total weight (mg)	Yol weig (mg
Bella coola	299.9(22.7)	2	138	20.7(1.5)	287.5(29.7)	178.7(
	8.38(0.29)	4	150	23.1(0.8)	286.3(24.8)	177.9(
		8	149	22.5(1.0)	302.1(20.6)	189.7(
		12	150	21.8(0.8)	296.2(27.3)	193.0(
Khutzeymateen	301.6(25.6)	2	83	20.6(1.5)	295.9(29.4)	184.5(
	8.54(0.32)	4	95	22.3(0.8)	276.2(24.2)	178.7(
		8	120	24.3(0.8)	305.0(26.9)	177.7(
		12	93	22.3(0.8)	285.4(21.8)	187.0(
Kshwan	327.6(14.3)	4	114	22.7(1.0)	293.8(18.3)	196.0(
	8.80(0.34)	8	119	22.7(1.2)	318.3(14.5)	217.0(
		12	120	21.9(1.1)	308.7(14.2)	212.5(
Stagoo	336.5(36.7)	4	42	22.2(0.9)	298.0(42.1)	198.6(
	8.78(0.44)	8	40	21.5(1.2)	293.4(34.0)	192.7(
		12	41	21.5(0.7)	286.6(36.8)	200.7(
Lagins	283.2(41.5)	4	60	24.4(0.8)	284.4(39.9)	143.5(
	8.41(0.44)	8	60	23.5(0.8)	279.1(31.4)	143.9(
		12	60	23.4(0.6)	281.7(32.9)	151.5(
Pallant	265.2(20.9)	4	149	23.7(1.0)	273.8(30.9)	154.2(
	8.21(0.32)	8	148	23.6(0.9)	279.2(27.4)	153.6(
		12	149	23.3(0.9)	268.0(27.9)	155.4(
Wannock	246.2(18.2)	4	149	21.7(0.6)	236.1(17.1)	144.9(
	7.98(0.32)	8	150	22.7(0.8)	243.5(27.2)	146.2(
		12	148	21.6(0.7)	241.9(21.0)	150.4(
Chemainus (early)	272.8(23.7)	4	150	22.3(0.7)	262.5(26.4)	161.5(
	8.21(0.32)	8	148	22.2(0.7)	251.8(24.7)	157.4(
		12	148	22.3(0.9)	269.2(27.4)	159.4(
Chemainus (late)	251.0(28.9)	4	148	21.3(1.0)	245.4(27.2)	142.2(
	7.99(0.28)	8	146	22.3(0.8)	253.8(26.2)	144.8(
		12	148	22.3(0.7)	238.9(20.6)	148.5(

tissue weights for chum salmon alevins and fry maintained at three or four controlled temper-
ined in each stock. Standard deviations are given in parentheses.

n		Fry				
Yolk weight (mg)	Tissue weight (mg)	*N*	Fork length (mm)	Total weight (mg)	Yolk weight (mg)	Tissue weight (mg)
178.7(20.2)	108.7(29.0)	150	34.0(2.3)	379.4(31.2)	49.2(33.8)	330.2(53.1)
177.9(14.7)	108.4(16.7)	150	35.1(1.0)	418.7(27.2)	54.1(19.6)	364.6(23.0)
189.7(16.7)	112.4(12.6)	151	36.1(0.8)	429.9(28.8)	27.4(12.8)	402.5(24.6)
193.0(17.5)	103.1(17.4)	149	34.9(1.5)	383.3(39.4)	18.2(10.9)	365.1(41.2)
184.5(17.9)	111.4(27.8)	94	33.2(3.0)	375.5(34.6)	61.3(38.7)	314.3(63.0)
178.7(17.7)	97.5(13.3)	105	35.6(1.0)	427.7(31.0)	48.7(11.2)	379.0(30.0)
177.7(15.6)	127.3(18.4)	120	35.5(1.3)	429.1(21.1)	48.4(31.8)	380.6(36.8)
187.0(17.0)	98.4(16.5)	112	36.2(1.4)	396.5(38.7)	15.9(10.8)	380.6(38.0)
196.0(11.4)	97.8(14.4)	109	36.2(1.0)	445.2(20.6)	42.2(12.5)	403.0(22.9)
217.0(34.5)	101.3(34.8)	120	35.8(0.8)	447.6(15.9)	58.6(9.2)	389.0(17.8)
212.5(11.1)	96.2(12.4)	120	35.6(2.4)	415.8(25.3)	25.8(10.2)	390.0(27.8)
198.6(29.7)	99.4(17.4)	47	36.2(1.2)	436.3(44.8)	36.6(16.8)	404.0(33.0)
192.7(19.9)	100.6(16.3)	60	35.2(1.4)	462.7(55.8)	67.2(13.5)	395.5(47.9)
200.7(17.9)	85.9(21.5)	45	36.2(1.2)	430.7(51.0)	27.1(16.5)	403.7(39.4)
143.5(20.8)	140.9(23.5)	60	35.3(0.9)	385.8(41.9)	25.8(15.5)	360.0(30.4)
143.9(24.6)	135.2(13.4)	60	33.7(0.7)	379.4(40.1)	36.0(15.1)	343.4(27.7)
151.5(21.5)	130.2(17.6)	60	32.6(1.2)	360.0(53.2)	42.0(10.8)	318.0(45.4)
154.2(13.9)	119.6(25.0)	150	35.7(1.1)	384.8(27.5)	34.6(8.2)	350.2(26.1)
153.6(13.2)	125.6(18.1)	150	32.7(0.8)	364.5(25.6)	60.6(14.8)	303.9(20.4)
155.4(11.9)	112.5(19.9)	150	32.5(1.7)	339.0(38.8)	42.0(11.1)	297.0(45.8)
144.9(14.1)	91.3(9.6)	150	34.1(0.9)	355.2(21.0)	37.1(10.0)	320.1(17.8)
146.2(17.5)	97.3(15.9)	150	35.1(0.9)	363.0(30.6)	17.7(10.3)	345.4(30.7)
150.4(12.6)	91.4(14.9)	150	32.5(1.2)	325.8(39.9)	38.8(10.1)	286.9(39.1)
161.5(16.6)	101.0(16.8)	150	35.5(1.1)	386.3(30.9)	40.3(10.4)	346.0(29.9)
157.4(18.1)	94.4(11.5)	150	34.4(0.9)	366.6(26.2)	43.6(10.5)	323.0(25.2)
159.4(15.9)	109.8(23.6)	150	34.1(1.1)	361.1(33.1)	32.5(10.0)	328.6(33.6)
142.2(15.1)	103.1(16.8)	149	33.7(1.3)	349.6(29.9)	32.7(11.0)	317.0(27.1)
144.8(15.8)	108.9(16.5)	150	34.5(1.1)	363.1(30.0)	32.3(11.0)	330.9(27.1)
148.5(14.8)	90.4(9.5)	150	33.4(1.0)	333.9(27.9)	33.8(7.7)	300.2(26.8)

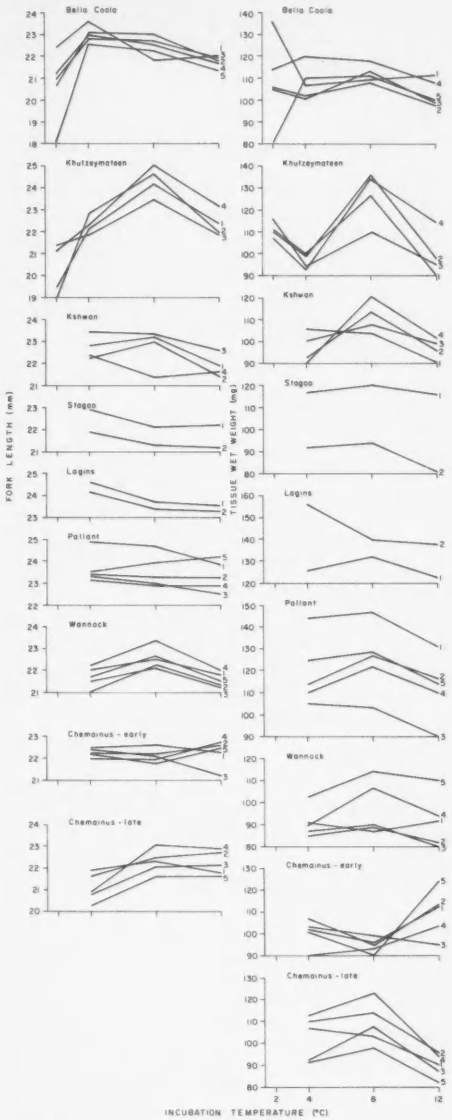

FIG. 5. Fork length and tissue weight of alevins at 50% hatching for 37 families from nine chum salmon stocks incubated at 2, 4, 8, and 12°C.

stocks are not similarly adapted to cope with a changing environment.

We investigated the efficiency of yolk conversion to body tissue during incubation of chum salmon alevins originating from stocks in both northern and southern British Columbia. At a common initial egg size, alevins from the northern and southern regions were of similar tissue weight when incubated at 4°C (108 and 105 mg, respectively) ($P > 0.10$), 8°C (114 and 122 mg, respectively) ($P > 0.10$), and 12°C (102 and 111 mg, respectively) ($P > 0.10$). Although not significant, there was a tendency for northern stocks to be more efficient at converting yolk to body tissue at 4°C than at higher incubation temperatures than were southern stocks.

Fry size

At a 2°C incubation temperature, fry length at emergence was the shortest and body tissue weight the lowest compared with other temperatures examined (Table 11). When all 17 stocks were compared for trends in fry fork length at the other three incubation temperatures, clear differences were found ($F_{2,32} = 5.25$, $P < 0.01$), with the longest fry produced at 8°C (35.9 mm), those at 4°C intermediate in length (35.6 mm), and those at 12°C the shortest (34.8 mm). Fry total weight varied similarly with incubation temperatures ($F = 6.23$, $P < 0.01$), with the rankings as with fork length (399, 391, and 380 mg, respectively). At emergence, there was no difference in the amount of residual yolk among temperatures ($F = 0.49$, $P > 0.10$), but there were clear differences in fry tissue weight ($F = 3.75$, $P < 0.01$), with the rankings of the incubation temperatures the same as for fry fork length and total weight (362, 353, and 342 mg, respectively). Incubation temperature had a marked effect on fry size at emergence, with the longest and heaviest fry produced at an 8°C incubation temperature.

Stock differences in fry length ($F_{16,59} = 3.51$, $P < 0.01$), total weight ($F = 2.40$, $P < 0.01$), and tissue weight were observed ($F = 3.29$, $P < 0.01$), but not for fry yolk weight at emergence ($F = 1.41$, $P > 0.10$). Fry from stocks with larger eggs (Kshwan, Stagoo) were larger than from those stocks with smaller eggs (Wannock, late Chemainus) (Table 11). Significant variation among females within stocks was observed for all fry size parameters (all $P < 0.01$) (Fig. 7), but as with alevins, these differences were attributable to variation in egg size among females.

Trends in fry size with respect to temperature were different among stocks. Significant interactions were observed between stock and incubation temperature for fry fork length ($F_{32,134} = 5.36$, $P < 0.01$), total weight ($F = 5.81$, $P < 0.01$), yolk weight ($F = 8.46$, $P < 0.01$), and tissue weight ($F = 5.47$, $P < 0.01$). Interactions between stock and temperature for fry length and tissue weight are clearly illustrated in Fig. 6. Jones Creek fry were the longest at 8°C, while those of Nitinat River and Pallant Creek were longest at 4°C, and Pallant Creek fry were the heaviest at 4°C, Jones Creek fry at 8°C, and Nitinat River fry at 12°C. Stocks clearly respond differently to incubation temperature with respect to fry size.

Trends in fry size with respect to incubation temperature varied among stocks, but also varied among families within a stock (all $P < 0.01$) (Fig. 7). The interactions between family and temperature were most apparent in the Kshwan and Khutzeymateen River stocks. Trends in fry size with respect to temperature can be dependent on both the stock and family under consideration.

There were regional differences in efficiency of conversion of yolk to body tissue for chum salmon stocks in northern and southern British Columbia. At a common initial egg size, chum salmon fry from northern stocks had greater tissue weight at emergence when incubated at 4°C than did fry from southern stocks (364 and 352 mg, respectively) ($F_{1,14} = 4.98$, $P < 0.05$). At 8°C, there was no difference in fry tissue weights between the two regions (360 and 369 mg, respectively) ($F = 0.37$, $P > 0.10$), and similarly at 12°C (342 and 341 mg, respectively) ($F = 0.00$, $P > 0.10$). Northern stocks were more efficient at converting yolk to body tissue at low incubation temperatures than were southern stocks.

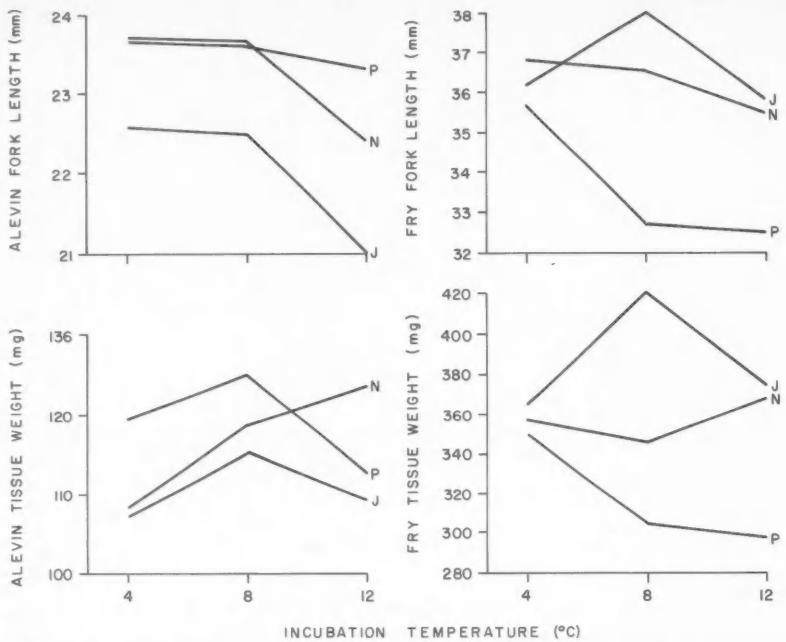

FIG. 6. Trends in alevin and fry fork length and tissue weight for three chum salmon stocks incubated at 4, 8, and 12°C. All families within stocks were pooled. Pallant Creek (P) is on the Queen Charlotte Islands, Nitinat River (N) is on the west coast of Vancouver Island, and Jones Creek (J) is a tributary of the Fraser River in southern mainland British Columbia.

Discussion

Given the diverse freshwater habitats that chum salmon are exposed to during their life cycle, and that stocks home to specific areas at specific times, selection should produce adaptations in stocks that are specific to the conditions that they encounter in their life cycle. These adaptations are only beneficial when expressed in suitable environments, and homing to natal rivers provides the opportunity for suitable environments to be encountered.

Male chum salmon are more abundant than females at the younger and older ages of maturity (Beacham and Starr 1982; Beacham 1984; this study), although Sano (1966) indicated that for Asian chum salmon, females predominate at ages ≥5 yr. The predominance of younger mature males is probably a result of sexual dimorphism in growth rates, with males growing faster than females (Sano 1966; Bakkala 1970). Body size is of considerable importance in determining a male's access to spawning females (Chebanov 1980; Schroder 1981; Chebanov et al. 1983), and the tendency for higher proportions of males at older ages may be a consequence of selection for larger body size in spawning males because they have an advantage over smaller males in competition for females during spawning (Schroder 1981).

Age at maturity in chum salmon is dependent both on timing of spawning (Koski 1975; Birman 1977; Beacham 1984) and stock abundance (Birman 1951; Helle 1979; Beacham and Starr 1982). Timing of spawning in Pacific salmon can have a genetic component (Bams 1976; Taylor 1980), as can age at maturity (Donaldson and Menasveta 1961; Ricker 1972). Age at maturity of chum salmon in British Columbia declines as the spawning season progresses, and as timing of spawning has a genetic component, variation in age at maturity of chum salmon can have a significant genetic component. Chum salmon from northern mainland British Columbia, spawning 2–3 mo earlier than chum salmon in southern British Columbia, are generally older than those in the southern region. Vitellogenesis in Pacific salmon begins during the decreasing photoperiod and temperature cycles of the autumn of the year prior to spawning (MacQuarrie et al. 1979), so that older ages at maturity in the northern mainland stock are not simply a reflection of the shortened growing period that northern stocks experience during their final year of ocean residence.

Regional differences in gillraker and branchiostegal ray number in chum salmon in British Columbia are apparent, with northern stocks generally having more of each than the southern stocks. Chum salmon on the west coast of Vancouver Island have more gillrakers and branchiostegal rays than those on the east coast of Vancouver Island, and thus are more like stocks from northern British Columbia. Gillraker number in Pacific salmon has both an environmental and genetic component (McCart and Andersen 1967; Beacham and Murray 1986b). Genetic variation in chum salmon is more closely associated with variability in meristic characters than in morphometric ones (Beacham and Withler 1985).

Chum salmon from large rivers were larger than those from small rivers at all ages of maturity, indicating an adaptation in growth rate to stream size. Water flows are generally more variable in small streams, and salmon in these streams can be more visible and accessible to predators than in large rivers. Smaller body size in these cases would be more advantageous than would large body size. Body size may also reflect gravel

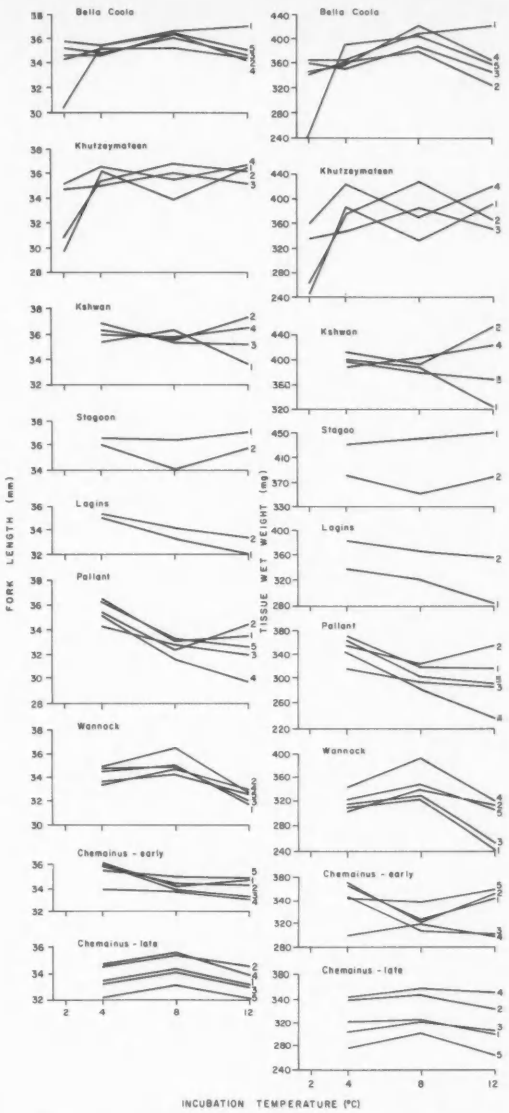

FIG. 7. Fork length and tissue weight of fry at 50% emergence for 37 families from nine British Columbia chum salmon stocks incubated at 4, 8, and 12°C since fertilization. Families within stocks are numbered from 1 to 5.

size within a stream. Large rivers usually have larger gravel than do small streams and a larger body size in females may be advantageous to properly dig and cover a redd during spawning. Many of the rivers in the Queen Charlotte Islands are classified as "small," and this probably explains the generally smaller body size of Queen Charlotte Islands chum salmon when compared with chum salmon in other areas of British Columbia.

Chum salmon spawning in small rivers have a shorter body length, smaller head, thinner caudal peduncle, and smaller fins than those spawning in large rivers. Eniutina (1954) suggested that salmon migrating longer distances up rivers had thicker, more muscular caudal peduncles than those migrating only a short distance, with the thicker caudal peduncle presumably allowing for more propulsion from the caudal fin. Larger fins would also be more effective than smaller ones in creating lift and providing propulsion during upstream migration.

At spawning, Pacific salmon are markedly sexually dimorphic, with differences in morphology and colouration usually allowing external visual identification of the sexes (Vladykov 1962; Beacham and Murray 1983). Sexual dimorphism in many morphometric characters has been reported, with males generally having larger heads, thicker caudal peduncles, and larger dorsal fins than females (Svetovidova 1961; Beacham 1984). Females have been reported to have larger anal fins than males (Berg 1979; Beacham 1984), and as females measure the depth of a nest with their anal fin (Tautz and Groot 1975; Schroder 1981), it is reasonable to expect that females would have larger anal fins than males.

Chum salmon may spawn at considerably different periods of the year in the same general region. Chum salmon can be separated into summer and autumn seasonal races, with the races differing in size, fecundity, and age at maturity (Sano 1966; Smirnov 1975). Timing of spawning can also vary considerably among autumn-spawning stocks, with stock differences in age at maturity and fecundity observed (Helle 1979; Beacham 1982, 1984). Initial incubation temperature can have a significant impact on subsequent embryo survival (Combs and Burrows 1957; Beacham and Murray 1986a), and our results generally suggest that embryos from late-spawning autumn chum salmon were more resistant to low initial incubation temperatures than were embryos from early-spawning stocks. However, there can be considerable variability in embryo survival at low incubation temperatures among late-spawning stocks. Late-spawning stocks frequently spawn in areas of groundwater upwelling (Smirnov 1975), and thus some stocks may never be exposed to low incubation temperatures. Embryo survival rates in our experiments were generally high, and incubation at threshold temperatures may be necessary to investigate differences in embryo survival rates among stocks spawning in different environments.

Chum salmon spawn during an extended period within a geographic area, but emergence of most of the fry from the redds and subsequent downstream migration occurs over a restricted time interval in the spring (Beacham and Starr 1982). Emergence timing of the fry is crucial, as survival of fry is related to timing of ocean entry (Walters et al. 1978). In order to synchronize fry emergence, stocks spawning at different times either spawn in areas of different water temperatures to standardize fry emergence timing, or the embryos and alevins have different rates of development that are stock specific, or both possibilities may exist. Fry from early-spawning stocks take longer to emerge than fry from late-spawning stocks. Early-spawning stocks are composed of more larger, older fish than are late-spawning ones, and these larger, older females produce larger eggs than the younger, smaller females in the late-spawning stock. Variation in egg size appears to be one mechanism by which fry emergence timing is regulated, but it is not the only mechanism. In our study, stocks with the largest eggs (Kshwan, Stagoo) produced fry emerging before those from Bella Coola and Khutzeymateen rivers; therefore, fry from the earliest-spawning stocks produced fry that took the longest time to emerge. Variation in egg size among females within a stock is not correlated with timing of fry emergence

(Beacham and Murray 1985b), which seems reasonable, considering that timing of fry emergence is critical to their susequent survival, and that there is an optimum time for fry emergence. Fry development rate has a significant genetic and environmental component, and variation in egg size among stocks is one method by which the genetic control on development rate is expressed.

Hatching time of alevins at each temperature was similar for all stocks that we examined, except for those stocks from the Queen Charlotte Islands, where hatching time was considerably later than in other stocks. Queen Charlotte Islands chum salmon stocks are quite distinctive genetically from stocks in other areas of British Columbia (T. D. Beacham, unpubl. data), presumably because the Queen Charlotte Islands was a refugium during the last ice age, while most other areas of British Columbia were glaciated (Warner et al. 1982). These stocks have had a longer period to accumulate genetic mutations. This long period of adaptation to the environment on the Queen Charlotte Islands, coupled with high mean winter water temperatures in these rivers (Anonymous 1977), may account for the differences in alevin hatching time between stocks in the Queen Charlotte Islands and in other areas of British Columbia.

Salmon stocks with larger eggs produce larger alevins and fry than do stocks with smaller eggs (Kazakov 1981; Wallace and Aasjord 1984; Beacham and Murray 1985b, 1986a). Size of alevins and fry is influenced not only by initial egg size, but also by the temperature regime during development. Adaptations of stocks to different temperatures are apparent, with northern stocks generally producing heavier alevins and fry at low incubation temperature (4°C) than southern stocks. Efficiency of enzymes in converting yolk to body tissue differs among the stocks, and the temperature of optimum yolk conversion efficiency for a species is not determined by examining the development of the progeny of a few individuals in one stock. Incubation environments vary considerably among stocks, and stocks do not respond identically to changes in incubation temperature.

We have demonstrated that chum salmon stocks in British Columbia differ in morphology and growth rates of the spawning adults, in age compositions of the spawners, in egg size of females at spawning, and in embryonic survival and subsequent development rate and size of alevins and fry. These differences are a result of selection which has produced stocks that are adapted to the environments that they encounter, and this has allowed chum salmon to exploit a wide variety of spawning habitats in British Columbia. Adaptation to specific environments may explain the largely unsuccessful transplants of Pacific salmon within what was thought to be their normal range (Helle 1981; Withler 1982). Transplants may be more successful if donor stocks are better matched to proposed environments. It is incumbent upon us in the management of chum salmon to ensure that the diversity of this species is maintained.

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References

ANONYMOUS. 1977. Water temperatures. British Columbia and Yukon Territory. Environment Canada, Inland Waters Directorate. 1874 p.

ARO, K. V., AND M. P. SHEPARD. 1967. Salmon of the North Pacific Ocean. Part IV. Spawning populations of North Pacific salmon. 5. Pacific salmon in Canada. Int. North Pac. Fish. Comm. Bull. 23: 225–327.

BAKKALA, R. G. 1970. Synopsis of biological data on the chum salmon, *Oncorhynchus keta* (Walbaum) 1972. U.S. Fish Wildl. Serv. Circ. 315: 89 p.

BAMS, R. A. 1976. Survival and propensity for homing as affected by the presence or absence of locally adapted paternal genes in two transplanted populations of pink salmon (*Oncorhynchus gorbuscha*). J. Fish. Res. Board Can. 33: 2716–2725.

BEACHAM, T. D. 1982. Fecundity of coho salmon (*Oncorhynchus kisutch*) and chum salmon (*O. keta*) in the northeast Pacific Ocean. Can. J. Zool. 60: 1463–1469.

1984. Age and morphology of chum salmon (*Oncorhynchus keta*) in southern British Columbia. Trans. Am. Fish. Soc. 113: 727–736.

BEACHAM, T. D., A. P. GOULD, AND A. P. STEFANSON. 1983. Size, age, meristics, and morphometrics of chum salmon returning to southern British Columbia during 1981–1982. Can. Tech. Rep. Fish. Aquat. Sci. 1207: 37 p.

BEACHAM, T. D., AND C. B. MURRAY. 1983. Sexual dimorphism in the adipose fin of Pacific salmon (*Oncorhynchus*). Can. J. Fish. Aquat. Sci. 40: 2019–2024.

1985a. Variation in length and body depth of pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) in southern British Columbia. Can. J. Fish. Aquat. Sci. 42: 312–319.

1985b. Effect of female size, egg size, and water temperature on developmental biology of chum salmon (*Oncorhynchus keta*) from the Nitinat River, British Columbia. Can. J. Fish. Aquat. Sci. 42: 1755–1765.

1986a. Comparative developmental biology of chum salmon (*Oncorhynchus keta*) from the Fraser River, British Columbia. Can. J. Fish. Aquat. Sci. 43: 252–262.

1986b. The effect of spawning time and incubation temperature on meristic variation in chum salmon (*Oncorhynchus keta*). Can. J. Zool. 64: 45–48.

BEACHAM, T. D., AND P. STARR. 1982. Population biology of chum salmon, *Oncorhynchus keta*, from the Fraser River, British Columbia. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 80: 813–825.

BEACHAM, T. D., AND R. E. WITHLER. 1985. Heterozygosity and morphological variability of chum salmon (*Oncorhynchus keta*) in southern British Columbia. Heredity 54: 313–322.

BERG, R. E. 1979. External morphology of the pink salmon, *Oncorhynchus gorbuscha*, introduced into Lake Superior. J. Fish. Res. Board Can. 36: 1283–1287.

BILTON, H. T., AND W. E. RICKER. 1965. Supplementary checks on the scales of pink salmon (*O. keta*). J. Fish. Res. Board Can. 22: 1477–1489.

BIRMAN, I. B. 1951. Qualitative characteristics of the stocks and dynamics of abundance of autumn chum salmon of the Amur River. Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okenogr. 35: 17–31. (Fish. Res. Board Can. Transl. 103)

1977. Intrapopulation groupings of the Amur autumn chum salmon, *Oncorhynchus keta*. J. Ichthyol. 17: 741–750.

CHEBANOV, N. A. 1980. Spawning behavior of the pink salmon *Oncorhynchus gorbuscha*. J. Ichthyol. 20: 64–73.

CHEBANOV, N. A., N. V. VARNAVSKAYA, AND V. S. VARNAVSKIY. 1983. Effectiveness of spawning of male sockeye salmon, *Oncorhynchus nerka* (Salmonidae), of differing hierarchial rank by means of genetic–biochemical markers. J. Ichthyol. 23: 51–56.

COMBS, B. D., AND R. E. BURROWS. 1957. Threshold temperatures for the

normal development of chinook salmon eggs. Prog. Fish-Cult. 19: 3–6.

DONALDSON, L. R., AND D. MENASVETA. 1961. Selective breeding of chinook salmon. Trans. Am. Fish. Soc. 90: 160–164.

ENIUTINA, R. I. 1954. Local stocks of pink salmon in the Amur basin and neighbouring waters. Vopr. Ikhtiol. 2: 139–143. (Fish. Res. Board Can. Transl. 284)

GODIN, J.-G. J. 1980. Temporal aspects of juvenile pink salmon (*Onchorhynchus gorbuscha* Walbaum) emergence from a simulated gravel redd. Can. J. Zool. 58: 735–744.

HELLE, J. H. 1979. Influence of marine environment on age and size at maturity, growth, and abundance of chum salmon, *Onchorhynchus keta* (Walbaum), from Olsen Creek, Prince William Sound, Alaska. Ph.D. dissertation, Oregon State University, Corvallis, OR. 118 p.

1981. Significance of the stock concept in artificial propagation of salmonids in Alaska. Can. J. Fish. Aquat. Sci. 38: 1665–1671.

HUBBS, C. L., AND K. F. LAGLER. 1958. Fishes of the Great Lakes region. University of Michigan Press, Ann Arbor, MI.

KAZAKOV, R. V. 1981. The effect of the size of Atlantic salmon, *Salmo salar* L., eggs on embryos and alevins. J. Fish Biol. 19: 353–360.

KOSKI, K. V. 1975. The survival and fitness of two stocks of chum salmon (*Oncorhynchus keta*) from egg deposition to emergence in a controlled-stream environment at Big Beef Creek. Ph.D. dissertation, University of Washington, Seattle, WA. 212 p.

LALANNE, J. J., AND G. SAFSTEN. 1969. Age determination from scales of chum salmon (*Oncorhynchus keta*). J. Fish. Res. Board Can. 26: 671–681.

MACQUARRIE, D. W., W. E. VANSTONE, AND J. R. MARKERT. 1979. Photoperiod induced off-season spawning of pink salmon (*Oncorhynchus gorbuscha*). Aquaculture 18: 289–300.

MCCART, P., AND B. ANDERSEN. 1967. Plasticity of gillraker number and length in *Oncorhynchus nerka*. J. Fish. Res. Board Can. 24: 1999–2002.

NEAVE, F. 1966. Salmon of the north Pacific Ocean. Part III. A review of the life history of north Pacific salmon. 6. Chum salmon in British Columbia. Int. North Pac. Fish. Comm. Bull. 18: 81–85.

PRITCHARD, A. L. 1943. The age of chum salmon taken in the commercial catches in British Columbia. Fish. Res. Board Can. Prog. Rep. Pac. Coast Stn. 54: 9–11.

RALEIGH, R. F. 1967. Genetic control in the lakeward migrations of sockeye salmon (*Oncorhynchus nerka*) fry. J. Fish. Res. Board Can. 24: 2613–2622.

REIST, J. D. 1985. An empirical evaluation of several univariate methods that adjust for size variation in morphometric data. Can. J. Zool. 63: 1429–1439.

RICKER, W. E. 1972. Hereditary and environmental factors affecting certain salmonid populations, p. 19–60. *In* R. C. Simon and P. A. Larkin [ed.] The stock concept in Pacific salmon. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver, B.C.

1980. Changes in the age and size of chum salmon (*Oncorhynchus keta*). Can. Tech. Rep. Fish. Aquat. Sci. 930: 99 p.

RUGH, R. 1952. Experimental embryology. Burgess Publishing Co., Minneapolis, MN. 480 p.

SANO, S. 1966. Salmon of the North Pacific Ocean. Part III. A review of the life history of North Pacific salmon. 3. Chum salmon in the Far East. Int. North Pac. Fish. Comm. Bull. 18: 41–57.

SATTERTHWAITE, F. E. 1946. An approximate distribution of estimates of variance components. Biom. Bull. 2: 110–114.

SCHRODER, S. L. 1981. The role of sexual selection in determining overall mating patterns and mate choice in chum salmon. Ph.D. thesis, College of Fisheries, University of Washington, Seattle, WA. 274 p.

SMIRNOV, A. I. 1975. The biology, reproduction and development of the Pacific salmon. Izd. Mosk. Univ. 335 p. (Fish. Mar. Serv. Transl. Ser. No. 3861)

SOKAL, R. R., AND R. J. ROHLF. 1981. Biometry. The principles and practice of statistics in biological research. W. H. Freeman and Company, San Francisco, CA. 859 p.

SVETOVIDOVA, A. A. 1961. Local stocks of summer chum salmon *Oncorhynchus keta* (Walbaum) of the Amur basin. Vopr. Ikhtiol. 17: 14–23. (Fish. Res. Board Can. Transl. 347)

TAUTZ, A. F., AND C. GROOT. 1975. Spawning behavior of chum salmon (*Oncorhynchus keta*) and rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 32: 633–642.

TAYLOR, S. G. 1980. Marine survival of pink salmon fry from early and late spawners. Trans. Am. Fish. Soc. 109: 79–82.

VLADYKOV, V. D. 1962. Osteological studies on Pacific salmon of the genus *Oncorhynchus*. Bull. Fish. Res. Board Can. 136: 171 p.

WALLACE, J. C., AND D. AASJORD. 1984. An investigation of the consequences of egg size for the culture of Arctic charr, *Salvelinus alpinus* (L.). J. Fish Biol. 24: 427–435.

WALTERS, C. J., R. HILBORN, R. M. PETERMAN, AND M. J. STALEY. 1978. Model for examining early ocean limitation of Pacific salmon production. J. Fish. Res. Board Can. 35: 1303–1315.

WARNER, B. G., R. F. MATHEWES, AND J. J. CLAGUE. 1982. Ice-free conditions on the Queen Charlotte Islands, British Columbia, at the height of the late Wisconsin glaciation. Science (Wash., DC) 218(4573): 675–677.

WITHLER, F. C. 1982. Transplanting Pacific salmon. Can. Tech. Rep. Fish. Aquat. Sci. 1079: 27 p.

Use of Small, Temporary, Floodplain Tributaries by Juvenile Salmonids in a West Coast Rain-Forest Drainage Basin, Carnation Creek, British Columbia

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Hartman, G. F., and T. G. Brown. 1987. Use of small, temporary, floodplain tributaries by juvenile salmonids in a west coast rain-forest drainage basin, Carnation Creek, British Columbia. Can. J. Fish. Aquat. Sci. 44: 262–270.

Seasonal movement of trout (*Salmo clarki* and *S. gairdneri*) into and out of three tributaries which drain areas ranging from 15 to 100 ha within the lower Carnation Creek catchment basin were monitored periodically from 1972 to 1985. The number of trout entering the three tributaries relative to total trout was as high as the number of coho salmon (*Oncorhynchus kisutch*) entering these tributaries relative to total coho. The percentage of the salmonid population represented by trout was highest in the two largest tributaries and lowest in the smallest. Trout were most clearly associated with nonvegetated sand and gravel bottom portions of the three tributaries. Coho were associated with this habitat too, but they also frequented portions of the tributaries that were vegetated and had a mud substrate. In the two largest tributaries, trout were represented by more age classes than were coho salmon. The paper considers some of the implications of use of small drainages by trout to habitat managers.

On a surveillé périodiquement de 1972 à 1985 le déplacement saisonnier de truites (*Salmo clarki* et *S. gairdneri*) entrant ou sortant de trois tributaires qui drainent des secteurs d'une superficie variant de 15 à 100 ha dans la partie inférieure du bassin hydrographique du ruisseau Carnation. Le nombre de truites entrant dans les trois tributaires par rapport au nombre total de truites était aussi élevé que le nombre de saumons cohos (*Oncorhynchus kisutch*) entrant dans ces tributaires par rapport au nombre total de ceux-ci. Le pourcentage de la population de salmonidés représenté par les truites était le plus élevé dans les deux plus gros tributaires et le plus faible dans le tributaire le plus petit. Les truites étaient très nettement associées aux secteurs des trois tributaires ayant un fond de gravier ou de sable non pourvu de végétation. Les saumons cohos étaient également associés à cet habitat, mais ils fréquentaient aussi des secteurs de ces tributaires pourvus de végétation et ayant un fond vaseux. Dans les deux plus gros tributaires, les truites étaient représentées par un plus grand nombre de classes d'âge que les saumons cohos. Dans cet article, on examine certaines des incidences de l'utilisation de petits bassins de drainage par la truite pour les gestionnaires de l'habitat.

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The use of a variety of habitat types adjacent to the main stream channel by juvenile coho salmon (*Oncorhynchus kisutch*) has been of considerable interest during the past 10 yr. The patterns of juvenile coho movement between main-channel locations and these habitats have been reported by Bustard and Narver (1975), Peterson (1980), Cederholm and Scarlett (1981), Scarlett and Cederholm (1984), Tschaplinski and Hartman (1983), and Bustard (1986). In the Carnation Creek (west coast of British Columbia) drainage system, habitats used by coho vary and include small seasonal streams a few hundred metres or less long which flow during the wet season and consist only of seeps and discontinuous pools in the dry season. They also include nonflowing flooded back channels, sloughs, and isolated oxbow ponds. In addition to these, the off-channel nonpermanent fish habitat includes areas of the floodplain which are periodically inundated during major winter storms (Brown 1985). Trout also use these habitats but not in the same way as coho.

The use of small tributary streams, 1–3 km^2, by trout has been documented. Hartman and Gill (1968) found cutthroat (*Salmo clarki*) and steelhead (*S. gairdneri*) trout in drainages of 1–2 km^2. They found that the species of trout in the tributary was governed by both the size and the profile of the tributary. In larger drainage systems, such as the south fork of the Hoh River and the Queets River in Washington, Sedell (1984) reported that coho were the most abundant salmonid in the terrace tributaries and the side channels whereas trout were the most abundant salmonid in the major tributaries and valley-wall tributaries. He also found that steelhead were the most abundant trout species in the lower reaches of the valley-wall tributaries whereas cutthroat were predominant in the upper reaches.

Cederholm and Scarlett (1981) found that both cutthroat and steelhead utilized riverine ponds as small as 0.85 and 1.29 ha and streams drainages 3 km^2 in area. Coho utilized both ponds and streams (Scarlett and Cederholm 1984), but trout were

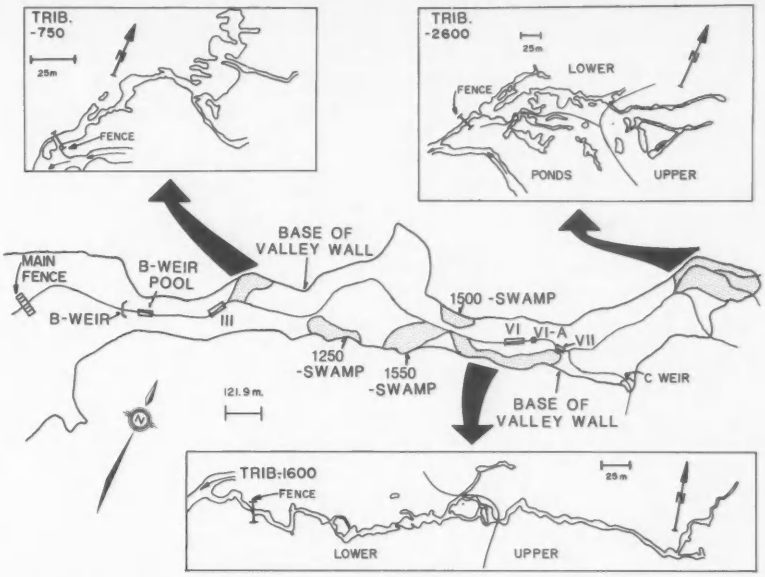

FIG. 1. Carnation Creek drainage from the high tide line to about 2900 m upstream. The floodplain, three study tributaries, and three swamps are indicated.

selective in habitat utilization. Cutthroat were more abundant in the riverine ponds whereas steelhead were more abundant in the two tributaries (Cederholm and Scarlett 1981). Most of these studies, however, are based on tributaries and ponds which are larger than the ones we studied.

The objectives of this paper are to (1) present information on the use of these very small tributaries by trout (*Salmo gairdneri* and *S. clarki*), (2) compare this information on trout with that published for coho, and (3) alert land managers to the potential importance of small tributaries and other seasonally inundated areas on the stream floodplain to salmonids.

The emphasis in this paper is on the use of small floodplain tributaries, 150–500 m long, by trout. There has been little information presented on the movement of trout to and from such a habitat or on their distribution within it. During the Carnation Creek project such information was gathered over many years and it is presented here.

Study Area

The study area included three minor tributaries, three small swamps, and the lower 3000 m of Carnation Creek, a 10-km^2 drainage on Vancouver Island, British Columbia (Fig. 1). Bustard and Narver (1975), Scrivener (1975), Hartman (1982), and Hartman et al. (1982) provided descriptions of Carnation Creek, and Andersen (1983, 1984) provided estimates of the fish populations in the drainage. Brown (1985) gave a detailed description of the minor tributaries and swamps with a characterization of salmonid habitat located within them.

Characteristics of each swamp and tributary section are summarized in Table 1. Tributary-750 is an abandoned mainstream channel and parallels the northern valley wall for approximately 150 m (Fig. 1). During winter storms, floodwater from the main channel mixes freely with tributary water through numerous channel scars. Water levels are seasonally variable. Winter water levels adequate to support overwintering salmonids are maintained by seepage from the valley walls, but in summer the tributary is totally devoid of standing water. The substrate consists of a blanket or veneer of organic soil (Canada Soil Survey Committee 1978), generally composed of fine sands and silts. This "muck" substrate covers the original gravel material within the abandoned channel. Vegetation rooted within the site is composed mainly of *Oenanthe sarmentosa*, *Scirpus microcarpus*, *Lysichiton americanum*, and *Typha latifola*.

Tributary-1600 borders the southern valley wall and is confined within a banked channel for most of its length of approximately 500 m (Fig. 1). The lower 250 m of the tributary contains standing water throughout the year, but during summer only isolated pools remain. Water velocities during winter storms are high enough to remove fine material and to prevent the establishment of rooted vegetation on the stream bottom, and the substrate consists primarily of exposed sand and gravel.

The substrate of the upper 250 m of Tributary-1600 consists mainly of a muck blanket supporting rooted semi-aquatic vegetation, similar to Tributary-750. Approximately 40% of the surface, however, is covered by intermediate sized woody debris (bark, broken limbs, and shattered log fragments). This upper section is completely dry during the summer months but maintains pools of standing water during the winter.

Tributary-2600 is approximately 400 m in length. The lower 250 m borders the northern and eastern walls of the floodplain and the upper 150 m is a relatively steeper section rising above the floodplain. In summer, pools of standing water exist throughout the main tributary channel, and in a few locations a flow is perceivable even during the driest summer months. The substrate is composed mainly of exposed sand and gravel. A series of small, vegetated, muck-bottomed ponds have formed within an abandoned channel parallel to the lower 100 m of Tributary-2600. These depressions are separated from the

TABLE 1. Features of minor drainages located on the Carnation Creek floodplain.

Minor drainage name	Length (m)	Section length (m)	Area flooded (m^2)[a]	Dominant substrate[b]	Rooted vegetation	Water table (cm)[c] Nov–Dec. 1982	Water table (cm)[c] July–Aug. 1983
Tributary-750	150		1000	Muck	Abundant	+16	−27
1250-swamp			1700	Muck	Abundant	+19	−9
1500-swamp			500	Muck	Abundant	+11	−12
1550-swamp			1500	Muck	Abundant	+24	+5
Tributary-1600	500	Upper 250	800	Muck	Abundant	+9	−11
		Lower 250	1100	Sand and gravel	Rare	+20	+14
Tributary-2600	400	Upper 150	800	Sand and gravel	Rare	+10	+6
		Lower 250	1700	Sand and gravel	Rare	+25	+17
		Ponds	800	Muck	Abundant	+17	−1

[a]Approximate area flooded at winter base flow.
[b]A muck substrate is defined as fine sand and silt material composed of greater than 30% organic material by weight.
[c]Measurements obtained from water table wells. Distance from soil surface to level of groundwater where "+" indicates water aboveground.

main channel except during floods.

Three small swamps (1250, 1500, and 1550) have formed within abandoned channels, paralleling the main channel of Carnation Creek. Vegetation, substrate, and seasonal water levels within these small swamps are similar to those found in Tributary-750, upper Tributary-1600, and Tributary-2600 ponds.

Materials and Methods

Visual Counts, Carnation Creek

Visual counts of juvenile coho and trout were made in Carnation Creek on 10 occasions from October 3, 1980, to March 20, 1981, by a swimmer using a snorkel and flashlight. The visual counts were made in five sections of the main stream. Four of these study sections, III, VI, VIA, and VII (62, 77, 8, and 27 m long, respectively) were located in permanent study areas where the regular May, July, and September population estimates were made (Andersen 1983). One study section, B-weir pool (38 m long), was located about 50 m upstream from hydrologic weir B (Fig. 1). The methods of counting fish are described in Tschaplinski and Hartman (1983). In the underwater surveys, upon which this paper is based, young of the year and fingerling trout were distinguished from coho salmon of corresponding size. Cutthroat trout could not, however, be distinguished from steelhead trout and the age of juvenile trout could not be reliably determined.

In this paper, "cover" consisted of either underbank space or debris piles. Volume of cover included the combined volumes of roots, and water space among the roots in the case of underbank cover. In the debris piles it included the volume of woody debris plus the water space in the debris pile. The volumes that were used in this study were those that were estimated to be available to fish at discharges of approximately 10 m^3/s. Cover volume was measured with a tape or metre stick and was accurate to within 0.5 m^3 for the large debris piles.

Population Estimates, Carnation Creek

Two population estimates were made in addition to those made annually in May, July, and September and are described in Andersen (1983). The additional population estimates were made in September and October 1980 in Sections III and VI for comparison with visual counts. Poleseine sampling in combination with electroshocking was repeated in a double removal method (Andersen 1983), and the statistical method used to estimate population size was from Seber and Le Cren (1967).

Trapping Fish Entering and Leaving Tributaries

Weirs, made with panels of galvanized or plastic 3.1-mm screen, and upstream and downstream traps were constructed and operated on Tributary-750, Tributary-1600, and Tributary-2600. The fish fence on Tributary-750 was installed at the beginning of September 1972 and operated during the following inclusive periods: September 1972 to February 1979, September 1979 to December 1979, September 1980 to October 1984, and April to June 1985. The fish fence on Tributary-1600 was installed in August 1972. It was operated for the following inclusive periods: August 1972 to June 1974, January and February 1980, September 1980 to December 1983, and April 1984 to June 1985. The fish fence on Tributary-2600 was installed in September 1982. It was operated from September 1982 to June 1985 inclusive. The traps occasionally did not function properly due to very low water or because of flooding past them.

Traps were usually checked every other day or daily during freshets and the numbers of coho and trout moving upstream and downstream were recorded. Fish were handled and measured as described by Tschaplinski and Hartman (1983).

The species of trout entering the traps as spawners were easily identified. The fry moving downstream following spawning were presumed to be progeny of the identified spawners. Intermediate-sized trout from 50 to 100 mm could not be identified with certainty.

No data were available on the actual discharges from the tributaries. An estimate of the seasonal water levels for each of the sites (Table 1) was obtained from a series of "water-level wells" situated within the sites (Brown 1985).

Trapping Fish within Offstream Sites

Estimates of the percentage of the salmonid population represented by trout within the various sites located on the Carnation Creek floodplain were obtained by fish capture using

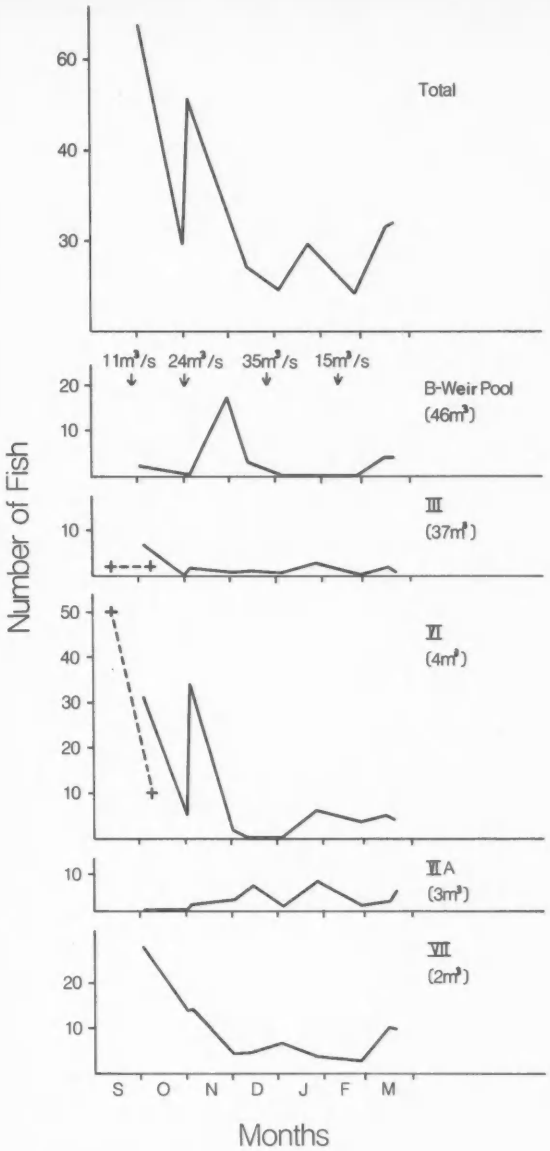

FIG. 2. Total counts and individual counts in study sections made by a swimmer from September 1980 to March 1981. Population estimated (broken lines) for Sections III and VI are based on the removal method with electroshocker and pole-seine. Volumes of flow and times of freshets are indicated by arrows.

baited minnow "Gee" traps. The method of trapping is given in more detail in Brown (1985).

Results

Visual Counts, Carnation Creek

The trout count in each of the five survey sections from October 1980 to March 1981 ranged from 0 to 34. The greatest change within the sites occurred between the beginning of October and the middle of December (Fig. 2). Counts in Sections VI and VII and the total count declined from October to mid-December. Counts of trout in Section VI, however, rose almost sixfold during a freshet (October 31 to November 2, 1980), and a similar increase occurred at the end of November in B-weir pool (Fig. 2). In the survey after the freshet, 32 of the fish counted in Section VI were seen in open riffle and pool locations where only 2 or 3 fish had been recorded before the freshet.

Trout numbers were highest in Sections VI and VII where the measured volumes of cover were 4 and 2 m^3, respectively. The section at the B-weir pool had 46 m^3 of cover but the count of trout in six of the surveys was two fish or less (Fig. 2). The upstream sections surveyed in this study tended to have more trout independent of section size or volume of the cover.

Population Estimates, Carnation Creek

The population estimate based on the removal method remained almost unchanged in Section III from September 16 to October 9, 1980, while the numbers in Section VI declined sharply in the same time period (Fig. 2).

Fish Entering and Leaving Tributaries

The mean monthly numbers of trout entering and leaving the tributaries were the lowest in Tributary-750 and highest in Tributary-1600. These means are based on 7.25, 5.7, and 2.8 yr of data for Tributary-750, Tributary-1600, and Tributary-2600, respectively (Fig. 3). The patterns of movement suggest higher net movement into all three tributaries during the September to February period and a somewhat higher rate of movement out of the tributaries during the March to June period (Fig. 3).

Some trout entered or left the tributaries in each month of the year and these movements involved fish ranging in age from 0+ to 3+ or 4+ yr (Fig. 4). Many of the older fish were spawners. Combined length frequencies of fish entering and leaving the three tributaries revealed several things about the size characteristics of the fish which were moving.

(1) From April until July, fry in the 20–29 mm range moved downstream. A smaller number of fish in this size range moved upstream from the mainstem and it is possible that some of these fish may have been migrants returning upstream through the traps.

(2) Many of the 0+ fish reached 70 mm by November and were still coming downstream at that time.

(3) In October there was active upstream movement into the tributaries, predominantly by fish in the 40–70 mm size range. The number of trout in the 100–150 mm range that moved upstream was about one quarter of that in the 40–70 mm size range.

(4) In November, fish in the 100–150 mm range were the major group moving upstream and fish in the 40–80 mm size range were less numerous (Fig. 4). This shift in the dominant size group of ascending fish was evident in data from both Tributary-1600 and Tributary-2600.

(5) In late October and November, larger trout (≥200 mm) began entering the tributaries. The largest fish moving upstream in the period from January to April were all cutthroat trout in spawning condition.

(6) In the 7.25 yr that the trap was operated on Tribu-

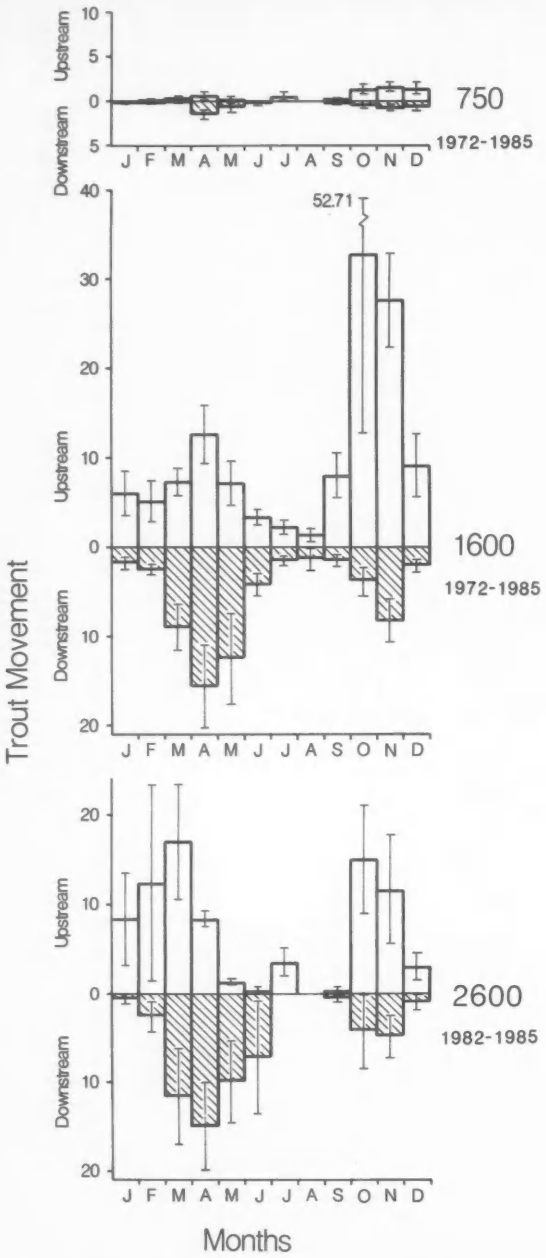

FIG. 3. Mean monthly numbers of trout (± SE) entering and leaving traps in Tributary-750, Tributary-1600, and Tributary-2600. Total duration of operation of traps was about 11.2, 6.7, and 2.6 yr for Tributary-750, Tributary-1600, and Tributary-2600, respectively.

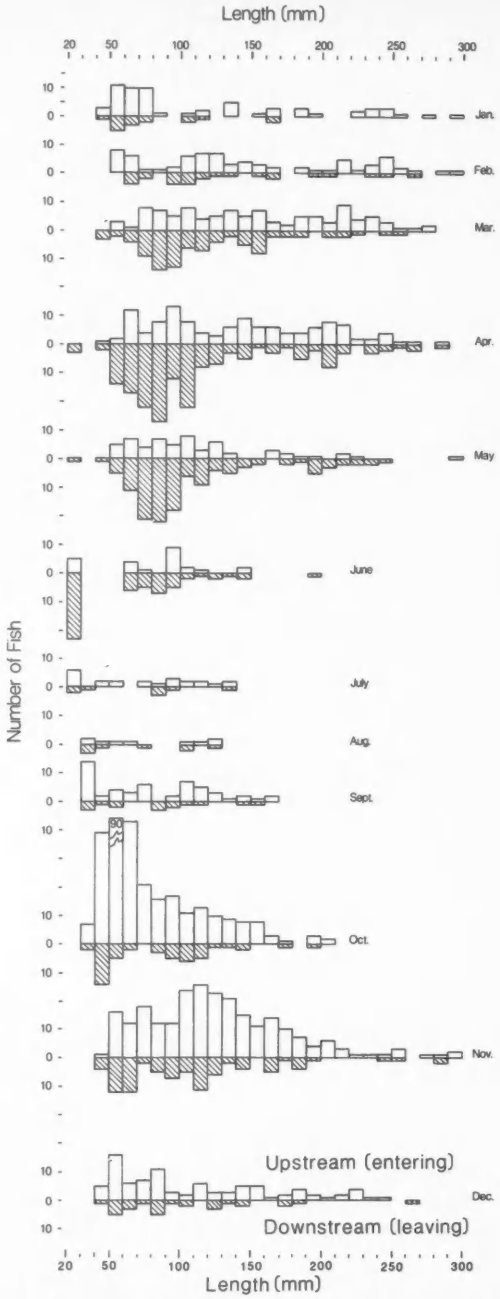

FIG. 4. Monthly length–frequencies of trout moving upstream (entering, open bars) and downstream (leaving, hatched bars). Data combined from Tributary-750, Tributary-1600, and Tributary-2600.

tary-750, only three trout over 200 mm long were captured going upstream.

Comparing the three tributaries, the lowest percentage of trout, expressed as a percentage of the numbers of trout plus coho, occurred in Tributary-750. The highest percentage of trout occurred in numbers entering and leaving Tributary-2600 (Fig. 5).

In the 3-yr period for which there were comparable data, trout made up a progressively larger fraction of the salmonids

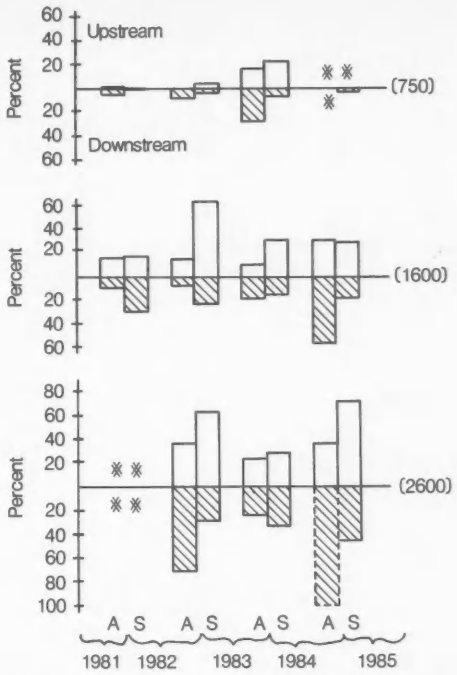

FIG. 5. Trout entering and leaving Tributary-750, Tributary-1600, and Tributary-2600 expressed as a percentage of the total number of salmonids (trout plus coho) entering and leaving. Autumn period A includes September to December; spring period S includes January to May. The double-X symbols indicate that the trap was not in operation. The histogram bar for the September to December period (A) in 1984 in Tributary-2600 is outlined by a broken line because only four fish were involved.

(coho plus trout) which entered and left Tributary-750, Tributary-1600, and Tributary-2600, respectively (Fig. 5). From the autumn of 1981 to the spring of 1985 (using both autumn and spring periods, Fig. 5), 7.3 and 9% of the salmonids entering and leaving Tributary-750, respectively, were trout. The corresponding percentages of salmonids that were trout were 27.4 and 20.6% entering and leaving Tributary-1600, respectively, 43.2 and 50.5% entering and leaving Tributary-2600, respectively.

In proportion to the number available in the lower 3000 m of stream, more trout than coho entered the three tributaries. The difference was not significant, however (paired t-test, $0.05 > p < 0.10$; Table 2). In Table 2 the numbers entering the three tributaries are expressed as percentages of the numbers of each species in the autumn population estimate, in the main creek.

A comparison of the percentage of salmonids represented by trout residing within three habitat types, for two winters (Table 3), indicates that trout use differed between these types (one-way ANOVA, $P < 0.05$). Percent trout within ephemeral sites was significantly lower than within both intermittent and mainstream sites (Scheffe's, $P < 0.05$) (Zar 1974). Trout use of ephemeral sites, when compared with coho use, was extremely limited (<1%), while use of intermittent tributaries and mainstream locations was much greater (25–37%).

Considering that trout densities may be higher in the upper half of the floodplain (B.C. Andersen, pers. comm. and unpubl. data), only those sites located within the upper two tributaries (1600 lower, 1600 upper, 2600 lower, and 2600 ponds) and closely situated mainstream locations (1600-1900 and 2500-2800) were compared. A significant difference (two-way ANOVA, $P < 0.01$) in percent trout use of the three habitat types was evident. Percent trout use of ephemeral habitat was significantly different from either intermittent or mainstream sites (Scheffe's, $P < 0.05$). No significant differences in percent trout between the three uppermost sites (2600 lower, 2600 ponds, and 2500-2800 mainstream) and the three sites associated with Tributary-1600 (1600 lower, 1600 upper, and 1600-1900 mainstream) were noted.

Discussion

The numbers of trout counted in the visual surveys (swimmer with a snorkel) were lower than the coho counts reported by Tschaplinski and Hartman (1983). The combined number of trout in the five visual counts in the mainstem of the creek fluctuated widely but declined during the period in which there was most movement into Tributary-1600 and Tributary-2600. Although the patterns of change in trout numbers for all five sections were erratic and inconsistent, the numbers were most variable in the late autumn. These observations, plus those made immediately after the late October freshet when fish were seen scattered along the stream bottom in Section VI, suggest that the autumn freshet period may be a period of movement and relocation for trout similar to that suggested for coho (Tschaplinski and Hartman 1983).

The abundance of trout in the visual count sections was not correlated with the volume of cover (Fig. 2) as was the case with coho (Tschaplinski and Hartman 1983). Sections VI, VIA, and VII had between 2 and 4 m^3 of cover during most of the visual count surveys but the numbers of trout were as high or higher than they were in the sections with 37 and 47 m^3 of cover.

The annual pattern of trout entry and exit to and from the three tributaries differed from that of coho and the difference was most pronounced in the late winter and early spring. About six times more coho and about five time more trout entered the tributaries than left in the autumn and early winter. In the late winter and early spring about five times more coho left the tributaries than entered them (Tschaplinski and Hartman 1983), while the numbers of trout entering and leaving were nearly equal (Fig. 3).

Direction of trout movement in the spring was less consistent than for coho. During this period, fish that appeared to be the same individuals, based on size, were noted to have moved upstream and back downstream within a span of a few days. There was concurrent upstream and downstream movement of trout 40–70 mm long which may have involved trout from the mainstem of the creek as well as from the tributary. Trout in spawning condition entered and left the tributaries in March, April, and May.

Trout were frequent users of the small tributaries studied. A similar or higher percentage of trout from mainstem population entered the three tributaries than was the case for coho (Table 2). Although a wider range of size and age groups of trout utilized the minor drainages than was the case for coho, trout did not utilize these offstream sites in the same way that coho did. As the size and permanence of the main tributaries decreased, the percentage of trout in the total number of fish entering them decreased (Table 3). Although the counting

TABLE 2. September 1982 and September 1983 population estimates of coho and trout in the mainstem of Carnation Creek and the percentage of each which entered the three tributaries in the autumn (Sept.–Dec.) and in the total autumn, winter, and spring period (Sept.–May).

	September pop. est		% coho		% trout	
Year	Coho	Trout	Sept.–Dec.	Sept.–May	Sept.–Dec.	Sept–May
1982	7 557	1456	3.7	5.2	5.3	14.5
1983	10 162	694	5.1	6.4	10.8	18.9

TABLE 3. Number of trout and coho captured and percent trout, within three habitat types, for specific sites sampled during winter 1983 and winter 1984.

		Jan.–Mar. 1983			Jan.–Mar. 1984		
Habitat type	Site	Trout *n*	Coho *n*	% trout	Trout *n*	Coho *n*	% trout
Ephemeral (muck substrate, vegetated swamps and tributaries	−750	0	240	0.0%	7	626	1.1%
	−1250	0	105	0.0	1	43	2.3
	−1500	—	—	—	0	156	0.0
	−1500	3	113	2.6	0	382	0.0
	−1600 (upper)	0	107	0.0	0	251	0.0
	−2600 (ponds)	3	43	6.5	4	96	4.0
Total		6	608	1.0	14	1554	0.9
Intermittent (sand and gravel substrate, nonvegetated tributaries)	−1600 (lower)	39	92	29.8	134	412	24.5
	−2600 (lower)	84	150	35.9	109	493	18.1
	−2600 (upper)	48	56	46.2	130	194	40.1
Total		171	298	36.5	373	1099	25.3
Mainstream	1600–1900	19	59	24.4	4	28	12.5
	1500–2800	29	37	43.9	50	132	27.5
Total		48	96	33.3	54	160	25.2

fences were inoperative during major freshets, we believe that they provided reliable indication of relative numbers of coho and trout occupying the tributaries. Trapping of salmonids, with baited minnow traps within the three tributary drainage areas, corroborated the fence trapping information which revealed lower use of Tributary-750 by trout. This information alone might suggest that low use of Tributary-750 by trout was only an artifact of its location nearer the downstream end of Carnation Creek. Other data in our study indicate that stream drainage area, stream permanence, flushing characteristics, and stream bottom type influenced fish distribution. The results from minnow trap sampling in Tributary-1600, Tributary-2600, and associated main channel locations indicated that trout were associated with those sections of the tributaries in which there was evidence of enough flow to scour the channel bottom and leave sand or gravel. Coho utilized a wider range of types of off-channel and small tributary habitat types. Coho were associated with the same habitats as trout as well as with areas of muck bottom and wetted vegetation. The low rate of entry by trout into Tributary-750, a wetted vegetation and muck bottom habitat, was consistent with their low use of similar habitats further up in the Carnation Creek drainage in upper Tributary-1600, the ponds in Tributary-2600, and the three minor swamps. Although the percentage of the salmonid population represented by trout may be higher in the upper half of the floodplain (B. C. Andersen, pers. comm. and unpubl. data), the longitudinal differences in abundance of trout along the mainstem of the creek were not the primary reason for the lower entry rate into Tributary-750.

This work has illustrated three points. First, trout (mainly cutthroat) and coho salmon enter and utilize very small drainages in the Carnation Creek basin. Second, trout are associated with specific parts of these small drainages and do not enter the less permanently flooded swamp areas with muck and vegetation bottom nor do they enter tributaries characterized by muck bottom only. Coho are associated with a wider variety of wetted habitats away from the main stem of the creek.

Although coho salmon and the two species of trout all occupy drainages less than 10 km^2, there is a great deal of diversity in their distribution. The diversity depends on season, drainage size, and drainage type and it is reflected further in the behavior of the fish. Hartman (1965) and Glova (1978, 1984) have shown that trout and coho are partially segregated into riffle and pool habitat. This segregation is interactive and it changes seasonally (Hartman 1965).

Although young trout and coho may share the same streams in various areas, it is clear that relative abundance of the two genera of salmonids depends on the nature of the tributary. Other research referred to in this paper and behavior studies (Hartman 1965; Glova 1978, 1984) show that there are a

variety of strategies that result in partial separation of the species. The habitat use pattern of trout and coho in very small (150-500 m long) drainages is another example of such partial separation.

Because a portion of coho and trout populations enters and utilizes very small drainages, a behavior which entails high risk in itself, it is urgent that human domestic and industrial activities in watersheds be planned to take such habitat use into consideration and to avoid compounding the risk. Cutthroat trout spawn and rear in small drainages and juvenile trout from the mainstem enter them over extended periods. This year-round pattern of use by one age group, or more, of trout causes the small drainages to be sensitive to human activities during all seasons. These considerations apply to tributary sections such as lower Tributary-1600 and upper and lower Tributary-2600.

There are special problems associated with the protection, during logging, of small tributaries such as those in the Carnation Creek floodplain. They may be so close together that trees cut along one tributary may fall into the next tributary and cross-channel yarding may be very difficult to avoid. The networks of ponds and channels may also be so extensive that they cannot be avoided if herbicides or pesticides are applied from the air.

There are a number of planning and management steps that can be taken to assist in the protection of small tributaries.

(1) Small tributaries should be mapped during the periods of high flow and clearly marked with surveyors ribbons. Location of seasonally wet swampy areas which are used by young coho in winter may be the most difficult part of the mapping.

(2) Roads should be located so that shallow groundwater seepage is not directed away from the tributaries. A characteristic of wall-base tributaries is that they are fed with water from such sources (Peterson and Reid 1984). If roads are built on the floodplain, the tributary crossings should be designed to permit movement of fish whenever it would naturally occur.

(3) Landing sites should be located away from small tributaries, and yarding across them should be minimized and so that the least amount of small debris is left in them.

(4) Yarding should be planned and carried out so that yarding scars and debris piles do not block the entrance to the small tributaries.

(5) Active logging should take place in the dry season when the swampy areas are dry and unoccupied by young coho. There may be difficulty in doing this because many of the logging companies prefer to use low-elevation floodplain sites for winter operations.

(6) In the postlogging periods, cedar salvage operations, for shake manufacture, should be located away from the small tributaries. Peterson and Reid (1984) reported cases where shake splitting waste and gravel pit overburden partly filled swampy habitat used by coho and made the habitat inaccessible.

(7) The application of herbicides, which would destroy aquatic plants, and insecticides should be planned to avoid small tributaries and swampy areas. This may require a more intricate layout of buffer strips and it may also require hand application of chemicals.

(8) Subdivision planners and agriculturists should be pursuaded, if possible, to minimize the ditching, dyking, and tunnel diversion of small tributaries and draining of small swamps.

It is clear that many small drainages, such as Tributary-750, Tributary-1600, and Tributary-2600 and the swamps at 1250, 1500, and 1550 m contribute to the production of trout and coho salmon. It is also clear that management and protection oriented primarily to large populations and stocks and the larger streams that support them might result in the progressive and cumulative loss of small drainages and the attrition of an important part of the salmonid resource.

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References

ANDERSEN, B. C. 1983. Fish populations of Carnation Creek and other Barkley Sound streams 1970–1980. Can. Data Rep. Fish. Aquat. Sci. 415: 265 p.

1984. Fish populations of Carnation Creek and other Barkley Sound streams 1981–1982. Can. Data Rep. Fish. Aquat. Sci. 435: 63 p.

BROWN, T. G. 1985. The role of abandoned stream channels as overwintering habitat for juvenile salmonids. M.Sc. thesis, University of British Columbia, Vancouver, B.C. 134 p.

BUSTARD, D. R. 1986. Some differences between coastal and interior streams and the implications to juvenile fish production. *In* Proceedings the Workshop on Habitat Improvements May 8–10, 1984, Whistler, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1483.

BUSTARD, D. R., AND D. W. NARVER. 1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board. Can. 32: 667–680.

CANADA SOIL SURVEY COMMITTEE. 1978. The Canadian system of soil classification. Can. Dep. Agric. Publ. 1646: 164 p.

CEDERHOLM, C. J., AND W. J. SCARLETT. 1981. Seasonal immigration of juvenile salmonids into four small tributaries of the Clearwater River, Washington, 1977–1981, p. 98–110. *In* E. L. Brannon and E. O. Salo [ed.] Salmon and trout migratory behaviour symposium, June 3–5, 1981. School of Fisheries, University of Washington, Seattle, WA 309 p.

GLOVA, G. F. 1978. Pattern and machanism of resource partitioning between stream populations of juvenile coho salmon (*Oncorhynchus kisutch*) and coastal cutthroat trout (*Salmo clarki clarki*). Ph.D. thesis, University of British Columbia, Vancouver, B.C.

1984. Managment implications of the distribution and diet of sympatric populations of juvenile coho salmon and coastal cutthroat trout in small streams in British Columbia, Canada. Prog. Fish-Cult. 46: 269–277.

HARTMAN, G. F. 1965. The role of behaviour in the ecology and interaction of underyearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 20: 1035–1081.

1982. The study area: an initial description, p. 15. *In* G. Hartman [ed.] Proceedings of the Carnation Creek Workshop, a 10 year review, February 24–26, 1982. Pacific Biological Station, Nanaimo, B.C. 404 p.

HARTMAN, G. F., B.C. ANDERSEN, AND J. C. SCRIVENER. 1982. Seaward movement of coho salmon (*Oncorhynchus kisutch*) fry in Carnation Creek, an unstable coastal stream in British Columbia. Can. J. Fish. Aquat. Sci. 39: 588–597.

HARTMAN, G. F., AND C. A. GILL 1968. Distribution of juvenile steelhead and cutthroat trout (*Salmo gairdneri* and *S. clarki clarki*) within streams in southwestern British Columbia. J. Fish. Res. Board Can. 25: 33–48.

PETERSON, N. P. 1980. The role of spring ponds in the winter ecology and natural production of coho salmon (*Oncorhynchus kisutch*) on the Olympic Peninsula, Washington. M.Sc. thesis, University of Washington, Seattle, WA. 96 p.

PETERSON, N. P., AND L. M. REID. 1984. Wall-base channels: their evolution, distribution, and use by juvenile coho salmon in the Clearwater River, Washington, p. 215–225. *In* J. M. Walton and D. B. Houston [ed.] Proceedings of the Olympic wild fish conference, March 23–25, 1983. Fisheries Technology Program, Peninsula College, 1502 E. Lauridsen Blvd., Port Angeles, WA 98362. 308 p.

SCARLETT, W. J., AND C. J. CEDERHOLM. 1984. Juvenile coho salmon fall–winter utilization of two small tributaries of the Clearwater River Jefferson County, Washington, p. 227–242. *In* J. M. Walton and D. B. Houston [ed.] Proceedings of the Olympic wild fish conference, March 23–25, 1983. Fisheries Technology Program, Peninsula College, 1502 E. Lauridsen Blvd., Port Angeles, WA 98362. 308 p.

SCRIVENER, J. C. 1975. Water, water chemistry and hydrochemical balance of dissolved ions in Carnation Creek watershed, Vancouver Island, July 1971–May 1974. Can. Fish. Mar. Serv. Tech. Rep. 564: 141 p.

SEBER, G. A., AND E. D. LE CREN. 1967. Estimating population parameters from catches large relative to the population. J. Anim. Ecol. 36: 631–643.

SEDELL, J. R. 1984. Habitats and salmonid distribution in pristine, sediment-rich river valley systems: S. Fork Hok and Queets River, Olympic National Park, p. 33–36. *In* W. R. Meehan, T. R. Merrell, Jr., and T. A. Hanley [ed.] Proceedings of a symposium fish and wildlife relationships in old-growth forests, April 12–15, 1982, Juneau, Alaska. Published by the American Institute of Fishery Research Biologists. 425 p. (Available from J. W. Reintjes, Rt. 4, Box 85, Morehead City, NC 28557).

TSCHAPLINSKI, P. J., AND G. F. HARTMAN. 1983. Winter distribution of juvenile coho salmon (*Oncorhynchus kisutch*) before and after logging in Carnation Creek, British Columbia, and some implications for overwinter survival. Can. J. Fish. Aquat. Sci. 40: 452–461.

ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall Inc., Englewood Cliffs, NJ. 620 p.

Effect of Stocking Density on the Survival, Growth, and Dispersal of Steelhead Trout Fry (*Salmo gairdneri*)

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In a coastal British Columbia stream a stocking density of between 0.3 and 0.7 fry/m^2 maximized the production of steelhead trout (*Salmo gairdneri*) parr and smolts. A severe autumn flood doubled the mortality rates of fry stocked at densities of 0.7 fry/m^2 or higher but had little effect on fry stocked at lower densities (<0.15 fry/m^2). Overall survival to smolts appeared to be lower than measured elsewhere for wild fish (2 vs. 4.5–18%). The proportion (<10%) of surviving fry found below the stocked sections was considered to be an indicator of potential displacement mortality in streams with no vacant downstream areas. This downstream dispersal was not density dependent and was small in comparison with the mortality of nondispersing fish. Although initial fry and parr sizes were density dependent, there was no detectable density effect on older parr or smolt sizes.

Dans un cours d'eau côtier de la Colombie-Britannique, une densité de repeuplement variant de 0,3 à 0,7 alevin/m^2 a maximisé la production de tacons et de smolts de truites arc-en-ciel (*Salmo gairdneri*). Une grosse inondation à l'automne a doublé les taux de mortalité d'alevins lorsque la densité était de 0,7 alevin/m^2 ou plus, mais elle a eu peu d'effet sur les alevins lorsque la densité de repeuplement était plus faible (<0,15 alevin/m^2). La survie globale des smolts a semblé plus basse que celle mesurée ailleurs pour les poissons sauvages (2 % par rapport à un pourcentage de 4,5 à 18 %). La proportion (<10 %) des alevins qui ont survécu trouvés en aval des secteurs ensemencés a été considérée comme un indicateur de la mortalité potentielle liée aux déplacements dans les cours d'eau où il n'y avait aucun secteur inoccupé en aval. Cette dispersion en aval ne dépendait pas de la densité et était faible en comparaison de la mortalité des poissons qui ne se dispersent pas. Bien que la taille initiale des alevins et des tacons dépendait de la densité, il n'y a eu aucun effet décelable de la densité sur les tacons plus âgés ou sur la taille des smolts.

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In this study, the effects of increased stocking density on subsequent growth, survival, and dispersal were investigated in juvenile hatchery-reared steelhead trout (*Salmo gairdneri*). Growth and survival in stream salmonids are apparently density dependent (Mills 1969; Wentworth and LaBar 1984). Previous studies of stocked unfed fry and planted eggs in related species have indicated that fry do not disperse well and most fry remain concentrated at high densities near the stocking point (Egglishaw and Shackley 1980; Mortensen 1977a). Lack of dispersal by stocked fry is therefore of interest, since both growth and survival of fry stocked at high densities should be reduced, even if unsaturated areas are available nearby. This connection between growth or survival and dispersal has not been examined in detail even though both dispersal and the density-dependent nature of growth and survival have both been the subject of various studies.

Lack of dispersal may have serious consequences for hatchery programs on streams, since point releases are often used for the enhancement of both anadromous and resident stream rainbow trout. For exmple, in British Columbia, 1.6 million 1- to 2-g steelhead fry are point stocked annually in 30 streams (B. Ludwig, B.C. Ministry of Environment, Victoria, B.C., pers. comm.). Average stocking densities, calculated using entire stream areas, are presumably low enough to ensure adequate growth and survival but it is important to determine whether dispersal from the individual point releases limits growth and survival.

Methods

Study Areas

The four streams selected for this study are located in the high rainfall area of the coastal mountains of southwestern British Columbia. The soils and their underlying rock are mostly granitic in origin, and as a consequence the nutrient content of the streams is generally low (Table 1). The climax forest cover is mainly western hemlock (*Tsuga heterophylla*) and Douglas fir (*Pseudotsuga menziesii*). All streams have barriers impassable to fish a short distance upstream from their mouths.

Lynn Creek is located in the District of North Vancouver (122°00′W, 49°20′N) and flows into Burrard Inlet. It was logged in the early 1900's but is now heavily forested. Lynn is the longest and widest of the study streams and the gradient within its study reach is the lowest (Table 1). Lynn had small resident populations of Dolly Varden (*Salvelinus malma*) (0.11/m^2) and cutthroat trout (*Salmo clarki*) (0.004/m^2) before the study began. Only historic daily flow records (1915–18)

TABLE 1. Morphology, water chemistry, and substrate composition of the four study streams.

	Lynn	Hastings	Liumchen	Tamihi
Morphology, whole stream				
Length (km)	19.6	4.1	12.3	17.0
Watershed area (km^2)	58.6	6.9	62.7	86.8
Maximum elevation (m)	1100	250	1450	1500
Morphology, study reach				
Watershed area (km^2)	39.7	5.9	58.8	78.7
Maximum elevation (m)	270	110	430	610
Gradient (%)	2.5	3.5	6.0	4.5
Wetted width (m)[a]	14	4	8	10
Water chemistry[b]				
pH	6.6–7.2	7.6–7.7	8.0–8.1	7.8
TDS (mg/L)	26	108	116	64
Soluble reactive phosphorous (mg/L)	<0.003–0.004	0.005–0.013	0.005–0.006	0.003
$NO^2 + NO^3$ nitrogen (mg/L)	0.10–0.27	0.33–0.55	0.07–0.09	0.05
Maximum temperature (°C)	18	16	18	13
Substrate composition[a]				
Fines 0–2 mm (%)	4	13	17	15
Gravel 3–64 mm (%)	26	43	21	19
Cobble 64–254 mm (%)	38	33	20	26
Boulders > 254 mm (%)	32	10	34	38
Bedrock (%)	0	0	8	0
D90 (m)[c]	1.1	0.5	1.1	1.7

[a]Means of census sites.
[b]Range from samples taken at various times in the summers of 1979–81.
[c]90th percentile of substrate diameter visually estimated by volume, i.e. 10% of the substrate is larger than this size.

are available for Lynn Creek. The mean annual daily discharge at the downstream end of our study section was 6.0 m^3/s^1 during this period. Lowest flows were always between August and October (0.04–0.42 m^3/s^1) but highest flows occurred in autumn, winter, or spring (36.5–84.4 m^3/s^1).

Rainfall records are available for the duration of this study from a site adjacent to the study area on Lynn Creek. An unusually high rainfall event occurred on October 30–31, 1981, when 285 mm of rain fell in 48 h. This is the highest 48-h rainfall recorded at this site since 1960, when records started, and double that of any similar period during the study. The October 1981 storm caused extreme flooding and extensive substrate movement and channel shifts in Lynn Creek. At one release site, for example, a large boulder (>6 m in diameter) was buried to a depth of 1.2 m by cobble and boulders up to 60 cm in diameter.

Hastings Creek enters Lynn Creek below the Lynn Creek barrier to anadromous fish. Although it is heavily wooded along its banks, over half of the watershed is residential area. It supported a relatively dense population of cutthroat trout ($0.75/m^2$). Flow was measured at 0.03 m^3/s^1 in August 1978, during the low summer flow period.

Both Liumchen and Tamihi creeks flow into the Chilliwack River, a tributary of the Fraser River, near Chilliwack (121°50′W, 49°05′N). Liumchen has a comparatively high nutrient content (Table 1) and was fishless prior to our study. The watershed was heavily forested and has not been logged for many years. Tamihi Creek drains the heavily logged watershed adjacent to Liumchen. This stream is glacier fed and, as a result, has the lowest maximum summer temperature (13°C) of the study streams and is slightly turbid throughout the year. Tamihi supports brook trout (*Salvelinus fontinalis*) in the upper part of the study reach ($0.04/m^2$) and resident rainbow trout throughout ($0.02/m^2$).

No daily flow data were available for either Liumchen Creek or Tamihi Creek. An August 1979 flow measurement in Liumchen was 0.5 m^3/s^1, while two measurements in Tamihi of 1.2 and 2.3 m^3/s^1 indicate that the glacier melt maintains relatively high summer flows in this stream. Rainfall records are available from Cultus Lake approximately 10 km west of Liumchen. Lowest rainfall is in the summer but major rainfalls can occur at any time of the year. The same storm that devastated Lynn in October 1981 also occurred at Cultus Lake. It did not, however, have a noticeable effect on the substrate in Liumchen Creek.

Experimental Design

Fry were fed in a hatchery for 1–2 mo and then released into small coastal streams. Density profiles and dispersal distances were measured for large groups of fry released at a single point. In addition, survival, growth, and emigration were estimated for three densities using groups of fry scattered over 700-m sections of streams.

Mature males and females were mainly obtained by angling downstream of the fish passage barriers. Fry were raised to release size (~1 g) in hatchery troughs at 9.5°C. All fry used in the experiments were marked before release with either a pelvic fin clip or fluorescent grit (Pribble 1976). The experi-

TABLE 2. Stocking and subsequent census times of the point released fry.

Stream	Release Date (d/mo/yr)	Site	Size (g)	Number	Census time since release: Fry (mo)	1+ parr (yr)	2+ parr (yr)
Lynn	17/8/78	4	0.7	3580	1.6	1.1	2.1
Lynn	17/8/78	5	0.7	3580	1.6	1.1	2.1
Hastings	17/8/78	1	1.0	400	1.1	0.8	
Hastings	17/8/78	2	1.0	400	1.1	0.8	
Hastings	8/8/79	3	1.0	2000	2.0		
Tamihi	30/7/79		0.2	7000	2.0		
Liumchen	17/7/78	1	1.2	1750		1.2	2.1
Liumchen	7/9/78	1	2.0	5140		1.0	
Liumchen	27/7/79	1	1.0	3110	2.6	1.2	2.3
Liumchen	27/7/79	2	1.0	3110	2.6	1.2	2.3

mental fry were transported to the streams in aerated fry cans (40 × 40 × 100 cm) or by tanker truck and released manually. Fry were either dispersed evenly throughout the stocking section (scatter release) or in groups at separate sites (point release).

Fry were point released in each stream during July and August (1978 and 1979) and September (1978) (Table 2). Sites upstream and downstream of the point release site were censused 1−3 mo later and 1−2 yr later.

The effects of stocking density on growth and survival were examined in Lynn Creek. In July 1979 the whole study reach (3 km) was scatter stocked with 1.2 g fry at 0.3 fry/m^2. This is close to the average density of wild fry found in British Columbia coastal streams (P. Slaney, B.C. Ministry of Environment, Vancouver, B.C., pers. comm.). In 1980 and 1981, 1.5- and 1.2-g fry, respectively, were scatter stocked at three densities in 700-m sections of the reach separated by at least 300 m. The densities were chosen to bracket average wild densities and to ensure a strong density-dependent effect. Each density group was marked with a different fluorescent grit colour. The sections were stocked at the following dates and densities:

Cohort	Density (fry/m^2): Low	Medium	High
August 14, 1980	0.14	0.72	~1.9
July 24, 1981	0.13	0.68	2.10

The release density for the high density section in 1980 was only an estimate because an oxygen stoppage in the tanker truck during the stocking operation necessitated point releasing two thirds of the fish at the top end of the section. The fry used in these experiments were approximately 50% from Lynn Creek and 50% from the Big Qualicum River on Vancouver Island. There were no consistent differences in growth and survival of the two stocks (distinquished by pelvic fin clips); therefore, they were treated as one stock in this report.

Population and Dispersal Estimates

Streams were sampled for population size and fish growth during September in Lynn Creek and July and August in the other streams. Sampling was done by replicated electrofishing "runs" in sites (12−25 m long) between a downstream stop-net and an upstream stop-net or natural obstruction. A "run" consisted of careful electrofishing upstream between the nets, followed by a quicker downstream sweep. In Lynn and Tamihi creeks, approximately 70% of the fish were captured in the downstream net. Three runs were done at each site.

In the dispersal studies, sites upstream and downstream of the release point were sampled starting near the release point. An attempt was made to sample at increasing distances from the release point both upstream and downstream until no more marked fish were captured. This was not always possible because of either time limitations or poor access to the streams. In the density study, three sites within each density section were censused and at least one site upstream and downstream of each section was also sampled.

Estimates of numbers at each site were made by the three-run DeLury declining catch method (Seber and LeCren 1967). The total population for each release group was determined by expanding the site densities using the following formula:

$$N_j = \sum_{i=1}^{n} D_i L_i P_{ij} M_j^{-1}$$

where N_j = population estimate for group j, D_i = *S. gairdneri* density (fish per linear metre) at site i, L_i = length of stream (metres) represented by site i, P_{ij} = proportion of site i catch belonging to group j, M_j = estimate of mark retention rate of group j determined from the mean of clipped fish that also had a fluorescent mark (rates used were 0.95, 0.83, and 0.71 for 0+, 1+, and 2+ fish, respectively), and n = number of sites.

An estimate of the standard error for N_j (S_{N_j}) can be calculated from

$$S_{N_j}^2 = \sum_{i=1}^{n} S_{\bar{D}_{ij}}^2 L_i^2 P_{ij}^2 M_j^{-2}$$

if it is assumed that M_j, P_{ij}, and L_i are known without error and a standard error for density ($S_{\bar{D}_{ij}}$) can be calculated.

The standard error in density within each 700-m section (stocked at a constant density) can be estimated as the variance among the three sites within the section. This standard error among sites within a section ($S_{\bar{D}_j}$) was releated to density (r^2 = 0.55, 0.92, and 0.96 for 0+, 1+, and 2+ fish, respectively) and therefore $S_{\bar{D}_{ij}}$ for sites outside the section were calculated from the regression between $S_{\bar{D}_j}$ and $\bar{D}_j$ for sites within the section stocked with group j as suggested by J. Berkowitz (Pacific Datametrics Consultants, Vancouver B.C., pers. comm.).

The population estimates were used to calculate instantaneous mortality rates (Z) per 30-d month, the results of which are presented as monthly mortality rates (A) where

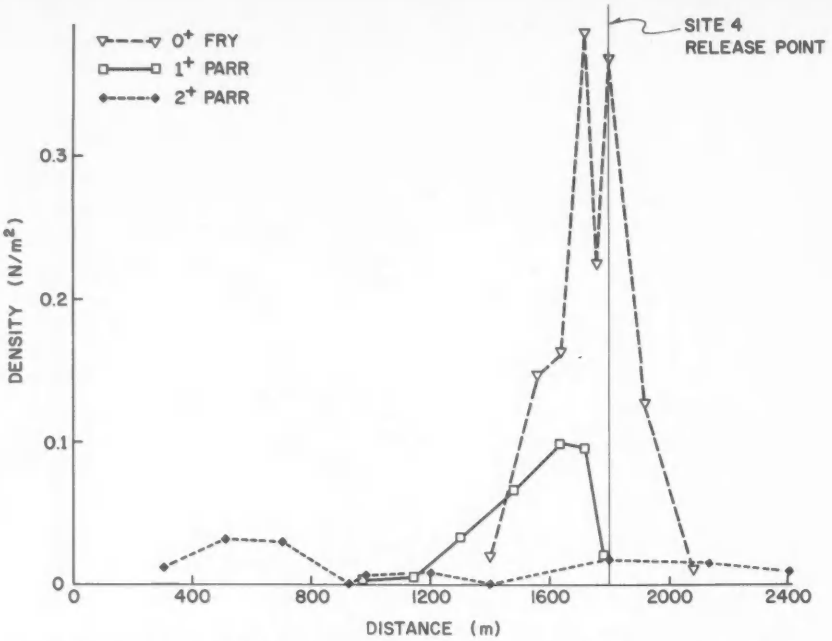

FIG. 1. Density profiles of fish from the site 4 release point in Lynn Creek on August 8, 1978. Fish were sampled on September 24–29, 1978 (0+); September 21–24, 1979 (1+); and September 15 – October 8, 1980 (2+). Distances are measured from the bottom end of the experimental section.

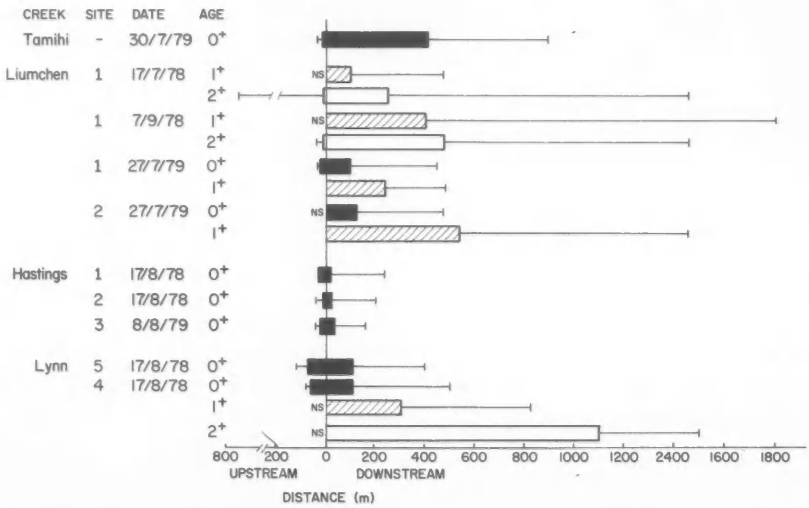

FIG. 2. Median (bars) and maximum (line) dispersal distances both upstream and downstream from the summer (July–mid-August) point release sites to the first (0+), second (1+), and third (2+) autumns after release. In some cases, upstream dispersal was not sampled (NS).

$$A = (1 - e^{-Z})\ 100.$$

Average census density for each group was determined from the mean of the densities of the three sites within each section, ignoring the sites outside of the stocking section.

Dispersal distances were estimated by first plotting a "density profile" consisting of the density of marked fish plotted against the distance from the release point. From this the maximum upstream and downstream dispersal distance could be measured or estimated and the median dispersal distance determined. Median dispersal distance was calculated by determining the area under the curve between the release point and the farthest upstream or downstream distance and then determining the distance from the release point that splits this

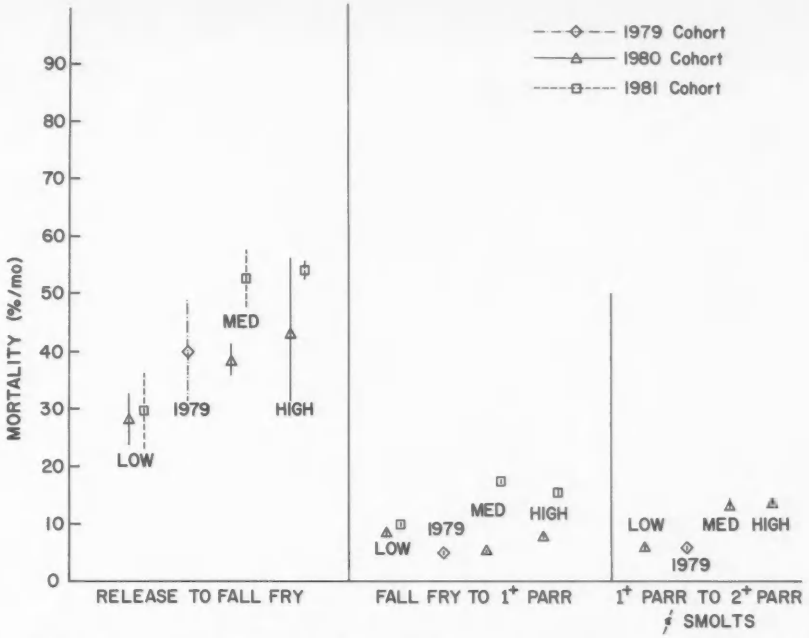

FIG. 3. Monthly mortality between census periods for the density experiments in Lynn Creek. Vertical lines indicate ±2 SE. Points are in order of increasing density and within each density by year.

area (= fish) into two equal parts. The median was arbitrarily chosen as a measure of the dispersal of the fish. A similar procedure was followed for dispersal from the ends of the scatter release sections (density experiments). In addition, the percentages of fish dispersing from the density sections were also calculated.

Migrating smolts in Lynn Creek were captured by a horizontal net trap suspended from overhead cables, approximately 3 km downstream of the bottom of the experimental section. It was in operation from April 24 to June 23, 1982. The trap fished the whole stream width, and fish collecting efficiency was determined by releasing marked steelhead smolts upstream of the net. This efficiency estimate (78.1%) was then used to expand the total catch for a smolt population estimate. Details of the net design, operation, and efficiency estimates are in Tsumura and Hume (1986).

Results

Dispersal from Point Releases

Typically, fry density, 1−2.5 mo after a point release of fry, was highest just downstream of the release site and then decreased rapidly both upstream and down (e.g. Fig. 1). By their second autumn the 1+ parr dispersed a greater distance but the highest density was still close to the release site and rapidly declined in both directions. By their third autumn, many of the 2+ fish had smolted and emigrated from the stream. In Lynn Creek there was little difference in density of 2+ parr throughout the sampling section, but in Liumchen the 2+ parr densities still peaked just downstream of the release site and declined rapidly in both directions as did the 1+ parr densities.

"Early fry" released into Tamihi Creek soon after they started feeding (0.2 g) in July dispersed more evenly and farther by the autumn than the "1-g" fry in other streams (Fig. 2). Density was approximately the same for the first 300 m downstream from the release site before declining rapidly. The median dispersal distance was 410 m.

In Hastings Creek, the smallest of the study creeks, the "1-g" fry had only dispersed a median distance of 25−40 m by the time of their first autumn in 1978. Most fish were clumped near the release sites and maximum dispersal was estimated to be only ≤240 m. Increasing the stocking density fivefold in 1979 did not increase the dispersal distance.

Dispersal of "1-g" fry was considerably farther by the first autumn in Lynn Creek. Both release groups had median dispersal distances of 130 m and estimated maximum distances of 400−500 m. By their second autumn the 1+ fish had almost doubled their dispersal distance to 280 m (median) and 850 m (maximum). Measurements of dispersal in the 2+ fish were difficult because many fish had already smolted and the overlap from the two release sites was extensive. However, the median distance was at least 1100 m for the fish from section 4.

In Liumchen "1-g" fry released into a previously barren section of the stream (1979, site 2) and into a section stocked the previous year (1979, site 1) had a similar dispersal distance of 100−130 m in the autumn of their first year and a maximum distance of 450−500 m. In their second autumn the pre-barren group had dispersed a median distance of 550 m and a maximum of 1450 m, while the prestocked group had only dispersed 250 m (median) and a maximum of 525 m.

In July 1978, 1750 1.2-g fry were point released into the previously fishless Liumchen, and in September another 5140 2-g fry were released at the same site. Neither group was sampled until they were 1+ parr. At that time the parr from the earlier release had a median downstream dispersal distance of only 100 m, while the parr from the later release had a median

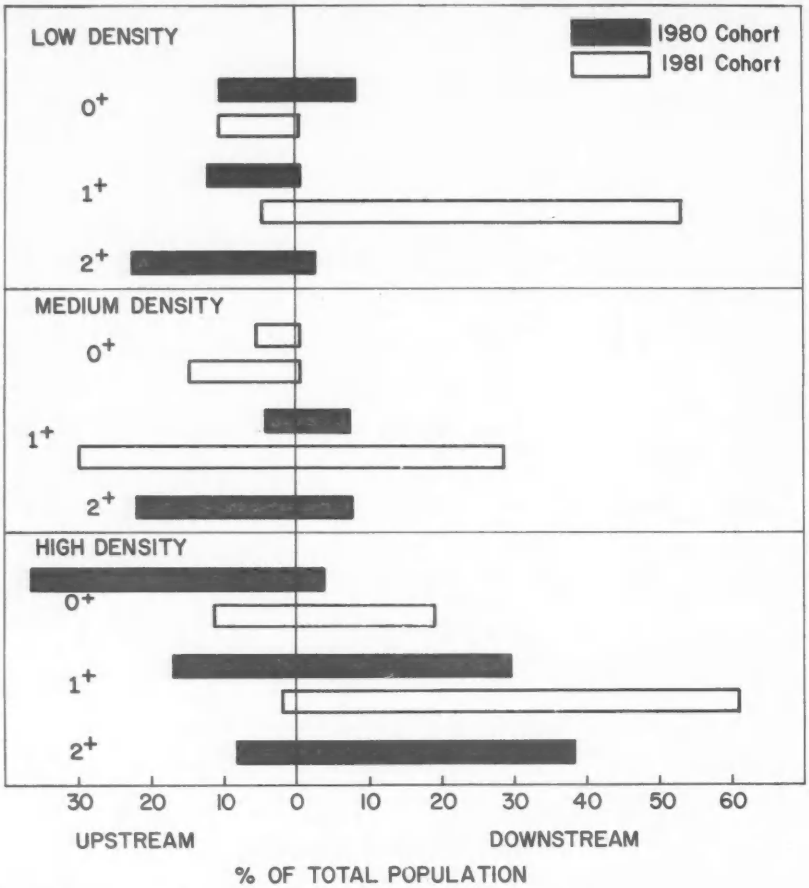

FIG. 4. Percent of populations captured outside the stocking sections for the density experiments in Lynn Creek.

distance of 405 m. As 2+ parr, the first release more than doubled their median dispersal to 250 m, but the later release had only slightly increased their dispersal distance to 475 m. There was little upstream movement of 2+ parr in Liumchen but a 450-g mature 2+ female from the early release was captured 750 m upstream.

Density Effects in the Scatter Releases

Mortality and dispersal

Mortality from release to autumn fry in Lynn Creek increased with increased stocking density, ranging from about 28% per 30-d month for the low-density groups to over 50% for the 1981 medium- and high-density groups (Fig. 3). The autumn 1+ parr stage showed little variation among densities for the 1979 and 1980 cohorts, ranging from 5.1 to 9.6%/mo for all four estimates. For the 1981 cohort, however, mortality to 1+ parr was about 10%/mo for the low-density group but greater than 15%/mo for the medium- and high-density groups. The 2+ mortality estimates for the 1980 cohort included parr and the catch from the smolt trap on Lynn Creek in 1982. Again, mortality rates increased with increasing stocking density, ranging from 6.0 to over 13%/mo for all density groups.

The overall mean survival rate from release to autumn 0+ fry was 49%, 68% for the low-density groups, and 30–48% for the other groups. Survival from release to 1+ parr ranged from 17 to 26% for the 1979 and 1980 cohorts and for the 1981 low-density group. However, the 1981 medium- and high-density groups had very low survival rates of less than 5%. Survival estimates of the 2+ parr and smolts (1980 cohort) were 12, 5, and 4% for the low-, medium-, and high-density groups, respectively.

For the 1981 cohort, medium- and high-density overwinter mortality rates from fry to 1+ parr were approximately double that of the 1980 cohort. This was associated with an unusually large flood event in October 1981 which caused extensive changes to and shifting of the stream channel.

Survival to 2-yr smolts was measured only in the spring of 1982 following the October 1981 flood event and therefore may be unusually low. They were only 1.4, 0.9, and 0.4% for the low-, medium-, and high-density groups, respectively. The 1982 smolt trap also captured smolts from the 1979 cohort with an estimated 3-yr smolt survival of 0.8% from release. As the parr survival estimates for this group were similar to the low-

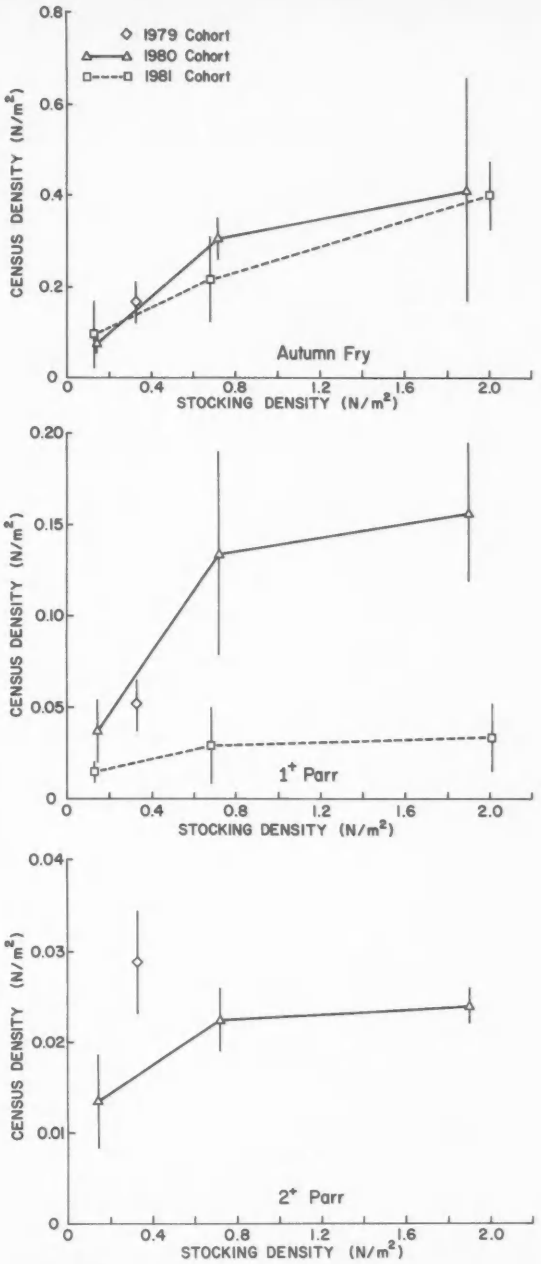

FIG. 5. Relationship between stocking density and subsequent census density on Lynn Creek with ±2 SE (vertical lines) for the density estimates.

density groups, we can tentatively combine the two smolt survival estimates to produce an overall smolt output of about 2% for the low-density group and lower for the other groups.

Fish captures below the stocking boundaries of the low- and medium-density sections were very low in 1980, less than 8% (Fig. 4). However, following the 1981 flood, 53 and 29% of the 1+ parr, from the 1981 low- and medium-density sections, respectively, were found downstream of their sections. Dispersal downstream from high-density sections was generally higher than in the other sections and highest for the 1981 1+ parr (4–61%). Upstream dispersal was generally higher but more variable than downstream, averaging 14.9, 11.7, and 17.5% for the 0+, 1+, and 2+ fish, respectively. There was no obvious pattern associated with density or age.

In general, dispersal distances were short. For example, no fry and few parr from the low-density release section were found more than 200 m downstream of the release section. Fry and parr from the high-density release group were found in small numbers up to 1 km downstream but no marked fish were found below that.

Higher census densities (fish per square metre) were correlated with higher stocking densities (Fig. 5) but the census density of autumn fry appeared to approach an asymptote at the higher stocking densities. In the 1+ and 2+ parr, the low-density release group had the lowest census density whereas there was little difference between the medium- and high-density groups within each cohort. The 1979 data fell between the low- and medium-density data for both fry and 1+ parr. The census densities of the medium- and high-density release groups were much lower in the 1981 cohort than in the 1980 cohort but only slightly lower in the low-density group.

TABLE 3. Comparison of fish weight among stocking densities within cohorts. Only fish stocked and captured within each density section are used in the comparison. Underlined means are not significantly different from each other (ANOVA and Duncan's multiple range test, $P < 0.05$).

Autumn fry			
1980	High	Low	Medium
g	2.49	3.63	3.80
n	80	59	92
1981	High	Medium	Low
g	2.84	3.44	3.47
n	109	73	51
Autumn 1+ parr			
1980	High	Low	Medium
g	11.2	12.7	14.1
n	74	17	47
1981	Medium	Low	High
g	15.3	15.4	15.6
n	7	7	35
2-yr smolts			
1980	High	Medium	Low
g	37.8	33.3	28.1
n	28	21	6
Autumn 2+ parr			
1980	High	Low	Medium
g	28.2	30.7	37.9
n	16	6	9

Growth

Autumn fry were the same size in the low- and medium-density groups but they were significantly smaller in the high-density groups (Table 3). Few significant differencs were found within the groups of 1- and 2-yr-old fish, but this may be partly due to small sample sizes. The inverse correlation between stocking density and size noted in the fry seems to be reversed in the smolts. However, sample sizes are small and differences are not statistically significant.

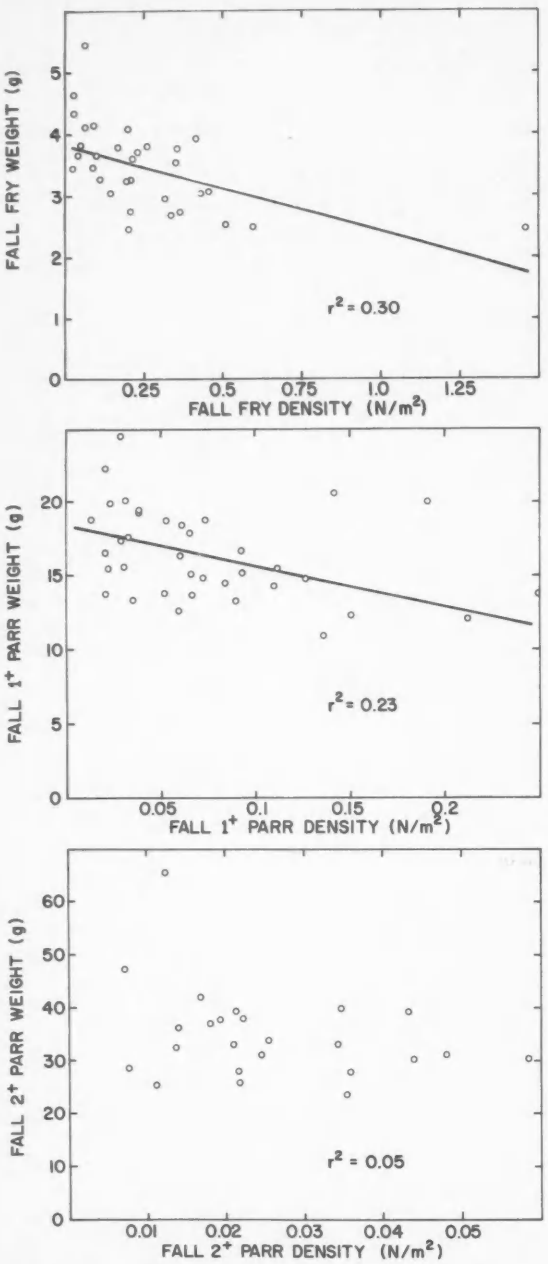
FALL FRY WEIGHT (g)
r^2 = 0.30
FALL FRY DENSITY (N/m²)
FALL 1⁺ PARR WEIGHT (g)
r^2 = 0.23
FALL 1⁺ PARR DENSITY (N/m²)
FALL 2⁺ PARR WEIGHT (g)
r^2 = 0.05
FALL 2⁺ PARR DENSITY (N/m²)

FIG. 6. Relationship between density and mean weight for all census sites on Lynn Creek from 1979 to 1982.

We also examined the relationship between density and mean weight of each age class at each census site. Although the coefficients of determination were small, linear regression analysis showed a significant negative correlation between size and census density for both the autumn fry and for the 1+ parr but not for the 2+ parr ($P < 0.05$, Fig. 6).

Discussion

Mortality of steelhead during their first summer increased at higher stocking densities. Similar results have been reported elsewhere for other stream salmonids (Table 4), but in most cases the density at which mortality increased was considerably higher than in this study. This was probably due to the higher productivity of those streams. Few fish were found further than 200 m downstream of stocking sections. Sampling was done for 4 km downstream, suggesting that very little of the loss could be attributed to emigration out of the study area.

Most of the parr mortality was density independent both in this study and in others (Table 4). However, mortality of parr between the autumns of 1981 and 1982 was higher and density dependent, probably caused by the major flood in late October 1981. There may have been differences in the amount of flood damage between sections, but we do not have the detailed habitat measurements necessary to document this. Floods can be a large source of mortality in stream salmonids (Allen 1951; Elwood and Waters 1969; Seegrist and Gard 1972; Hoopes 1975).

Assuming little movement between sites, there was a weak but significant relationship between site density and autumn fry or autumn 1+ parr size, indicating that growth was density dependent. This relationship was not evident for the autumn 2+ parr census, probably because of migrations of the larger smolt and increased parr movements between sites. Density-dependent growth responses have also been demonstrated in Atlantic salmon (*Salmo salar*) by Backiel and LeCren (1967) and Egglishaw and Shackley (1977, 1980), in brown trout (*Salmo trutta*) by Mortensen (1977b), and in coho salmon (*Oncorhynchus kisutch*) by Scrivener and Andersen (1984).

Survival and, to a lesser extent, growth of fry were reduced by high density because the fry did not move into adjacent vacant areas. For point released fry, median dispersal distances over the summer were typically <100 m and densities remained high near the stocking location. Migrations can be an important part of the freshwater life of many stream salmonids (Solomon and Templeton 1976; Bjornn 1971). Fry and parr from a number of stocks may move out of summer rearing areas and into winter habitats in the autumn (Chapman and Bjornn 1969; Bjornn 1971; Randall and Paim 1982). Downstream migration of fry immediately following emergence from the gravel is common (LeCren 1973; Mortensen 1977a; Mills 1969; Randall 1982) but there is also a tendency to remain in one location (Edmundson et al. 1968; Cargill 1980; Slaney et al. 1980). In our study the dispersal of point released unfed fry in one stream was three times greater than those of fry which were held for 1−2 mo in the hatchery before being released into another stream, indicating that a tendency to disperse may be present only in newly emerged fry.

The similar dispersal distances of both the large and the small point releases in Hastings Creek (Fig. 2) suggest that fry do not respond to even very high densities. The sharp peak in the density profiles also indicates a lack of response to high densities, since such a response should have produced a flatter peak.

The small number of fry which moved out of the stocked sections in their first summer were included in the population estimates for this study. If the adjacent vacant areas were not available, such fish could become nomads and then would continue moving downstream to die in the ocean (Chapman 1962; Slaney and Northcote 1974). Thus, we could use the

TABLE 4. Mortalities of rainbow trout (Rb), Atlantic salmon (As), and brown trout (
theses (recalculated from the cited papers). Density dependence is indicated with the
density was used.

			Fry				
			Spring–summer		Spring–autumn		
Species	Source	Release date	Mean	Density dependence	Mean	Density dependence	M
Rb	0.2-g fry	May 16			31 (28–35)	Yes (0.8–1.8)	
As	Wild	July					(1
As	0.2-g fry	May			27 (22–35)	Yes (3.8–29.3)	
	Eggs	April			27 (26–28)	Yes (0.3–1.2)[a]	
As	0.2-g fry	May			29 (18–40)	Yes (2.0–6.2)	
As	0.2-g fry	May			48 (24–67)	Yes (1.7–15.5)	
As	0.2-g fry	Spring					
Bt	Eggs	May 7	54	na (9.0)			
Bt	0.2-g fry	May 6	29	na (25.0)			
Bt	Wild	Apr 15	22 (9–41)	Yes (3.1–18.0)			
Bt	Wild	Apr 15	9 (9–9)	No (2.1–3.1)			

[a]Egg plants, values used are densities at this end of the time period.
[b]Combined value for the 0.2-g fry and egg plant groups.

trout (Bt) from early fry to later fry and to 1-yr-old parr. Means are in % mortality/mo with a range in paren-
with the range of fish densities (fish/m^2) at the start of each period given in parentheses. na = only one stocking

			Fry to parr				
	Summer–autumn		To spring parr		To autumn parr		
ce	Mean	Density dependence	Mean	Density dependence	Mean	Density dependence	Reference
			16 (14–17)	No (0.15–0.19)			Wentworth and LaBar 1984
	30 (12–42)	Yes (1.8–12.0)			16 (13–24)	No (0.9–3.1)	Egglishaw and Shackley 1977
							Egglishaw and Shackley 1980
					8[b] (1–12)	No (0.3–2.9)	
					8 (4–12)	No (0.1–0.8)	Anonymous 1982
							Mills 1969
					14 (10–19)	No (0.2–2.5)	Elson 1975
	12	na (1.6)	6	na (1.2)			Mortensen 1977a
	5	na (1.3)					Mortensen 1977a
							Mortensen 1977b
							Mortensen 1977b

proportion of surviving fry that moved out of stocked sections as an index of "disperser mortality." This would only be an index because some dispersing fry may not be true nomads, since they only moved a few metres out of the section (thus inflating the estimate of disperser mortality) and some nomads died after dispersing into vacant areas (thus deflating disperser mortality).

Disperser mortality was low relative to both the total mortality and the number of nondispersing survivors. Disperser mortality was not density dependent. If only downstream dispersers were counted (coho nomads typically move downstream), less than 10% of the surviving fry moved out of the section and this proportion was not dependent on density (Fig. 4). In the low-density section (the least extreme case), total mortality was about 30% of the initial number stocked (Fig. 3) whereas the number of surviving downstream dispersers was only about 3% of the initial number stocked.

The results from Lynn Creek suggest that in similar streams, stocking densities for maximum smolt yield should be between 0.3 and 0.7 fry/m^2, since higher stocking densities did not result in much higher autumn fry or parr densities. Symons (1979), for comparison, recommended egg deposition densities of less than 2 eggs/m^2 for Atlantic salmon under most conditions. If egg to fry mortality is taken into account, then this represents at most only a slightly higher density than our recommendation. The low dispersal of fry suggests that stocking sites should be less than 500 m apart in order to fully utilize the capacity of the stream.

Data are not available for steelhead, but a number of studies on Atlantic salmon, which occupy a similar ecological niche, have demonstrated differences in aggression and feeding behavior of hatchery-raised and wild fish (Sosiak et al. 1979; Dickson and MacCrimmon 1982). Therefore, our results may only be applicable to hatchery fish, since fry which have been reared at high densities in a hatchery may have less of a tendency to disperse than wild fry. Greater dispersal of wild than hatchery fry has been reported for small groups of fish stocked at the same point (Symons 1969). However, some inferences concerning wild populations can still be made, since dispersal is often limited in natural situations (Cargill 1980; Edmundson et al. 1968), and more extensive movements are often associated with migration between spawning, rearing, and overwintering areas (Bjornn 1971; Solomon and Templeton 1976). In most other studies (Table 4), eggs or unfed fry were planted or observations were made on wild populations, but in our study the high mortality of emerging fry (LeCren 1973) is excluded. It should be noted that the mortality rates of our hatchery-experienced fish are similar to those in other studies using natural populations.

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References

ALLEN, K. R. 1951. The Horokiwi Stream: a study of a trout population. Fish. Bull. N.Z. 10: 1–238.

ANONYMOUS. 1982. Ecology and production of juvenile salmon. Smolt enhancement in the Tummel Valley, p. 19–22. *In* Triennial review of research. Dep. Agric. Fish. Scotland, Freshwater Fish. Lab., Pittochry.

BACKIEL, T., AND E. D. LECREN. 1967. Some density relationships for fish population parameters, p. 261–293. *In* S. D. Gerking [ed.] The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford.

BJORNN, T. C. 1971. Trout and salmon movements in two Idaho streams as related to temperature, food, stream flow, cover, and population density. Trans. Am. Fish. Soc. 100: 423–438.

CARGILL II, A. S. 1980. Lack of rainbow trout movement in a small stream. Trans. Am. Fish. Soc. 109: 484–490.

CHAPMAN, D. W. 1962. Aggressive behaviour in juvenile coho salmon as a cause of emigration. J. Fish. Res. Board Can. 19: 1045–1080.

CHAPMAN, D. W., AND T. C. BJORNN. 1969. Distribution of salmonids in streams, with special reference to food and feedings, p. 153–146. *In* T. G. Northcote [ed.] Symposium on salmon and trout in streams. Inst. Fish., University of British Columbia, Vancouver, B.C.

DICKSON, T. A., AND H. R. MACCRIMMON. 1982. Influence of hatchery experience on growth and behaviour of juvenile Atlantic salmon (*Salmo salar*) within allopatric and sympatric stream populations. Can. J. Fish. Aquat. Sci. 39: 1453–1458.

EDMUNDSON, E., F. E. EVEREST, AND D. W. CHAPMAN. 1968. Permanence of station in juvenile chinook salmon and steelhead trout. J. Fish. Res. Board Can. 25: 1453–1464.

EGGLISHAW, H. J., AND P. E. SHACKLEY. 1977. Growth, survival and production of juvenile salmon and trout in a Scottish stream, 1966–75. J. Fish Biol. 11: 647–672.

1980. Survival and growth of salmon, *Salmo salar* (L.), planted in a Scottish stream. J. Fish Biol. 16: 565–584.

ELSON, P. F. 1975. Atlantic salmon rivers, smolt production and optimal spawning: an overview of natural production. New Engl. Atl. Salmon Restor. Conf. Spec. Publ. Ser. No. 6: 96–119.

ELWOOD, J. W., AND T. F. WATERS. 1969. Effects of floods on food consumption and production rates of a stream brook trout population. Trans. Am. Fish. Soc. 98: 253–262.

HOOPES, R. L. 1975. Flooding as the result of hurricane Agnes, and its effect on a native brook trout population in an infertile hardwater stream in central Pennsylvania. Trans. Am. Fish. Soc. 104: 96–99.

LECREN, E. D. 1973. The population dynamics of young trout (*Salmo trutta*) in relation to density and territorial behaviour. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 164: 241–246.

MILLS, D. H. 1969. The survival of hatchery reared salmon fry in some Scottish streams. Dep. Agric. Fish. Scot. Freshwater Salmon Fish. Res. Rep. No. 39: 12 p.

MORTENSEN, E. 1977a. The population dynamics of young trout (*Salmo trutta* L.) in a Danish brook. J. Fish Biol. 10: 23–33.

1977b. Density dependent mortality of trout fry (*Salmo trutta* L.) and its relationship to the management of small streams. J. Fish Biol. 11: 613–617.

PRIBBLE, J. 1976. Pressure spray marking of fish with granular dyes. Dep. Fish Wildl. Oreg. Inf. Rep. Ser. Fish. No. 76-1.

RANDALL, R. G. 1982. Emergence, population densities, and growth of salmon and trout fry in two New Brunswick streams. Can. J. Zool. 60: 2239–2244.

RANDALL, R. G., AND U. PAIM. 1982. Growth biomass and production of juvenile Atlantic salmon (*Salmo salar* L.) in Miramichi River, New Brunswick, tributary streams. Can. J. Zool. 60: 1647–1659.

SCRIVENER, J. C., AND B. C. ANDERSEN. 1984. Logging impacts and some mechanisms that determine the size of spring and summer populations of coho salmon fry (*Oncorhynchus kisutch*) in Carnation Creek, British Columbia. Can. J. Fish. Aquat. Sci. 41: 1097–1105.

SEBER, G. A. F., AND E. P. LECREN. 1967. Estimating population parameters from catches large relative to the population. J. Anim. Ecol. 36: 631–643.

SEEGRIST, D. W., AND R. GARD. 1972. Effects of floods on trout in Sagehen Creek, California. Trans. Am. Fish. Soc. 101: 478–482.

SLANEY, P. A., S. J. BILLINGS, AND H. A. SMITH. 1980. Experimental stocking of steelhead fry above barriers in a high gradient tributary of the Keogh River: progress 1978 and 1979. Fish Wildl. Br. Fish. Tech. Circ. No. 41: 28 p.

SLANEY, P. A., AND T. G. NORTHCOTE. 1974. Effects of prey abundance on density and territorial behaviour of young rainbow trout (*Salmo gairdneri*) in laboratory stream channels. J. Fish. Res. Board Can. 31: 1201–1209.

SOLOMON, D. J., AND R. G. TEMPLETON. 1976. Movements of brown trout *Salmo trutta* L. in a chalk stream. J. Fish Biol. 9: 411–423.

SOSIAK, A. J., R. G. RANDALL, AND J. A. MCKENZIE. 1979. Feeding by hatchery-reared and wild Atlantic salmon (*Salmo salar*) parr in streams.

J. Fish. Res. Board Can. 36: 1408–1412.

SYMONS, P. E. K. 1969. Greater dispersal of wild compared with hatchery-reared juvenile Atlantic salmon released in streams. J. Fish. Res. Board Can. 26: 1867–1876.

1979. Estimated escapement of Atlantic salmon (*Salmo salar*) for maximum smolt production in rivers of different productivity. J. Fish. Res. Board Can. 36: 132–140.

TSUMURA, K., AND J. M. B. HUME. 1986. Two variations of a salmonid smolt trap for small rivers. N. Am. J. Fish. Manage. 6: 272–276.

WENTWORTH, R. S., AND G. W. LABAR. 1984. First year survival and growth of steelhead stocked as fry in Lewis Creek, Vermont. N. Am. J. Fish. Manage 4: 103–110.

Abundance Estimation of a Dispersed, Dynamic Population: Hooded Seals (*Cystophora cristata*) in the Northwest Atlantic

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Bowen, W. D., R. A. Myers, and K. Hay. 1987. Abundance estimation of a dispersed, dynamic population: hooded seals (*Cystophora cristata*) in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. 44: 282–295.

Pup production of hooded seals (*Cystophora cristata*) in the Northwest Atlantic was estimated by aerial survey. Simultaneous surveys and the collection of ground-truth data were conducted in March 1984 in both major whelping areas, namely the floe ice in the Davis Strait and off northeastern Newfoundland (the Front). Abundance estimates were obtained from both fixed-wing photographic and helicopter sighting surveys using a strip survey method for unequal-sized sampling units. These abundance estimates were corrected to account for pups which had left the ice and those pups which had yet to be born in each area. A maximum likelihood method was used to combine estimates of abundance from several surveys with estimates of the number of pups in each developmental stage to obtain an estimate of total production. This method weighted each survey point estimate of abundance by the estimated sampling variance and each estimate of the proportion of pups on the ice in each stage by the sample size corrected for loss of degrees of freedom associated with the sampling design. Total production at the Front was estimated to be 62 400 with 95% confidence limits of 43 700 to 89 400 and in the Davis Strait was 19 000 with a 95% confidence interval of 14 000 to 23 000. Total pup production estimates for the Front and Davis Strait are likely underestimates for several reasons, but are substantially higher than those previously assumed for the Northwest Atlantic.

On a déterminé par relevé aérien le nombre de nouveaux-nés du phoque à capuchon (*Cystophora cristata*) dans l'Atlantique nord-ouest. En mars 1984, on a effectué simultanément des relevés et des vérifications au sol dans les deux principales zones de mise bas, soit les glaces flottantes du détroit de Davis et la zone du Front au large de la côte nord-est de Terre-Neuve. Les estimations de l'abondance ont été obtenues à partir de relevés photographiques par avion et de relevés visuels par hélicoptère menés selon la méthode en bandes pour des unités d'échantillonnage de différentes tailles. Ces estimations ont été ajustées afin de tenir compte des nouveaux-nés qui avaient déjà quitté la banquise et ceux qui n'étaient pas encore nés dans chaque zone. On s'est servi d'une estimation de la valeur la plus probable pour obtenir une estimation de la production totale à partir des estimations de l'abondance obtenues de plusieurs relevés et des estimations du nombre de nouveaux-nés à chaque stade de croissance. Cette méthode a permis de pondérer chaque estimation ponctuelle de l'abondance en fonction de la variance estimative des échantillons ainsi que chaque estimation du pourcentage de nouveaux-nés présents sur la banquise à chaque stade en fonction de la taille de l'échantillon corrigée de la perte de degré de liberté liée à la conception expérimentale. La production totale sur le Front s'élève donc à 62 400 dans les limites de confiance à 95 % allant de 43 700 à 89 400 tandis que dans le détroit de Davis, elle s'élève à 19 000 avec des intervalles de confiance à 95 % variant de 14 000 à 23 000. Les estimations de la production totale sur le Front et dans le détroit de Davis sont probablement des sous-estimations pour plusieurs raisons quoiqu'elles soient nettement supérieures à celles supposées antérieurement pour l'Atlantique nord-ouest.

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Hooded seals (*Cystophora cristata*) whelp on floe ice during March mainly in three areas in the North Atlantic: near Jan Mayen Island, off northeastern Newfoundland (an area known as the Front), and in the Davis Strait (Sergeant 1975, 1976). After breeding, hooded seals migrate to moult on the pack ice east of Greenland in Denmark Strait between 66 and 68°N (Rasmussen 1960) and between 72 and 76°N (Sergeant 1974, 1976) during June and July. The genetic relationship and size of these three populations are uncertain (Rasmussen 1960; Sergeant 1974, 1978; Wiig and Lie 1984). This has generated concern about the impact of commercial hunting at Newfoundland and at Jan Mayen on trends in the population size of hooded seals in all three breeding areas.

Catches of hooded seals off Newfoundland were unregulated, in practice, prior to 1974 when the first catch quota of 15 000 animals was introduced, although regulations were already in place to enforce opening and closing dates of hunting. The first quota of 15 000 was based on the belief that the 1966 catch of 16 000 pups was too high and that therefore the catch had to be limited to less than the 1966 harvest (Anonymous 1973). Sustainable yield calculations were made in 1975. These and later calculations depended heavily on an estimate of average pup production for the late 1960s using the survival

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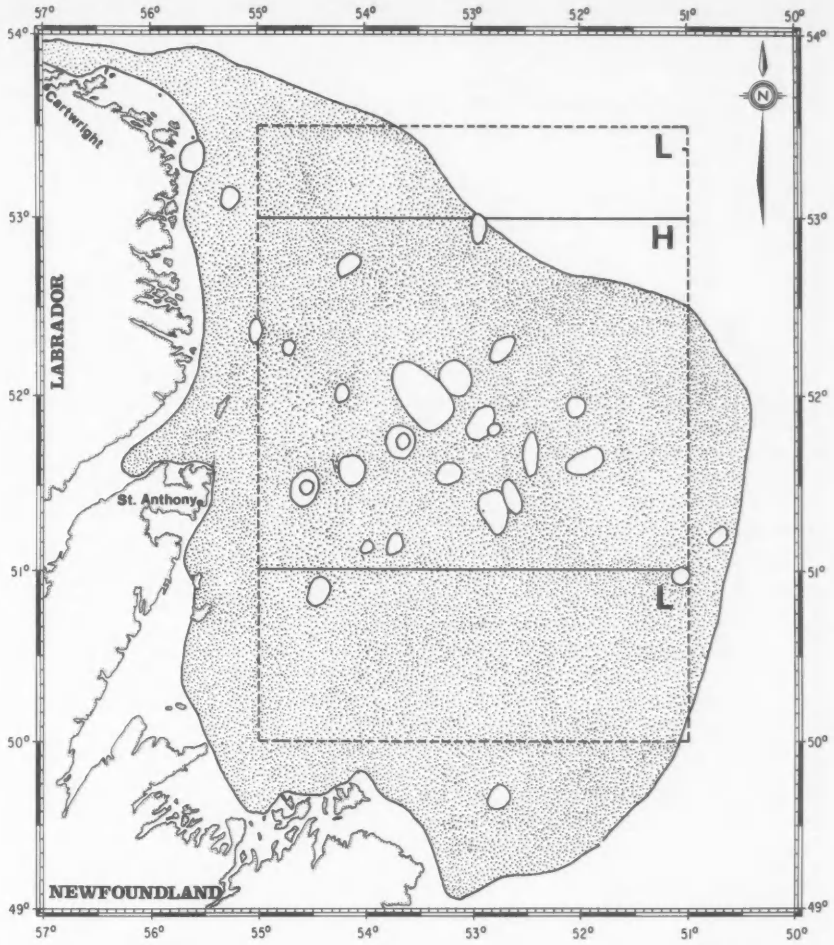

FIG. 1. Historical distribution of hooded seal concentrations at the Front during 1973–83. Approximate size and shape of whelping concentrations are shown as enclosed regions. The stippled region represents the distribution of the scattered hooded seal families. The study area of the 1984 survey is indicated by the broken box, and the solid horizontal lines demarcate the high (H) and low (L) density strata.

index method (Øritsland and Benjaminsen 1975; Sergeant 1975; Winters and Bergflødt 1978). The calculations became subject to increasing error as the estimate was projected forward to obtain an estimate of current stock size (Anonymous 1983). Between 1975 and 1982, catches at Newfoundland varied from 10 393 to 15 611 (Anonymous 1985). However, due to poor markets for pelts, catches after 1982 declined greatly to only several hundred animals or less. Hooded seals were not hunted in whelping concentrations off Newfoundland during our study in March 1984. Whelping concentrations in Davis Strait have not been commercially hunted.

The purpose of the present study was to estimate pup production in the Northwest Atlantic by conducting simultaneous aerial surveys in the Davis Strait and at Newfoundland. Previous attempts to estimate pup production in the Davis Strait (Sergeant 1974, 1976, 1977; MacLaren Atlantic Ltd. 1977; MacLaren Marex, Inc. 1979) and at Newfoundland (Hay and Wakeham 1983a) have suffered from logistic, design, and weather problems with the result that none have yielded reliable estimates of total pup production.

There is a large literature on strip- and line-transect methods for estimating animal abundance (Norton-Griffiths 1975a; Burnham et al. 1980). These methods have been most successful when used to estimate the abundance of large terrestrial mammals (generally ungulates) where all members of the population are available to be surveyed at one time if not one place (Siniff and Skoog 1964; Goddard 1969; Norton-Griffiths 1973, 1975b; Sinclair 1973). However, both strip- and line-transect methods may fail to give reliable results if only part of the population is available to be surveyed at one time or place, or if the entire population is present only for a short period of time. An example of this type of problem is the estimation of whale abundance (Doi 1974).

The estimation of hooded seal abundance in the Northwest Atlantic is also difficult for several reasons. First, hooded seals are a highly migratory, pelagic species. Pups are born on heavy

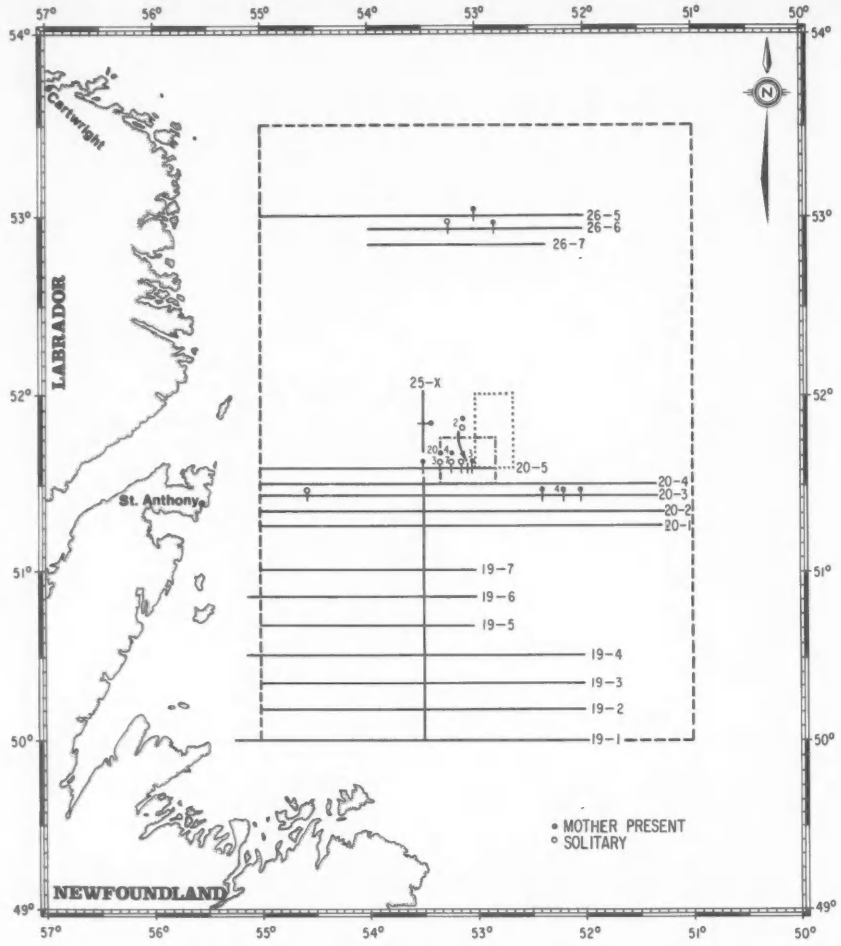

FIG. 2. Transects flown at the Front during March 1984. Observations of hooded seal pups (from the spot-photographs) are indicated along these transects. Transects are identified by date and a serial number. The dotted box outlines the hooded seal concentration on 25 March, and that with alternating dashes and dots outlines the concentration on 20–21 March.

born on heavy ice floes approximately 60–130 km off the southern coast of Labrador and up to 300 km offshore in the Davis Strait. Older hooded seals cannot be surveyed reliably because an unknown fraction migrate south to winter feeding and breeding areas or are on the ice at any point in time. Second, although most pups are born in concentrated areas, others are born widely scattered in areas of low density. Third, it is difficult to locate the pupping concentrations. Over 50 000 km^2 of suitable ice is present at the Front in most years, an area roughly the size of Ireland, and over four times this area could be considered suitable habitat in the Davis Strait. Further, having once located concentrations of pups is no guarantee that they will be found again, as ice drift can be considerable (i.e. 30–50 km/d). Finally, pups begin to leave the ice after only 4 d of lactation (Bowen et al. 1985); hence, any single survey will be incomplete because some pups will have left the ice, while others are yet to be born. Given these problems, it is clear that traditional survey designs are inadequate for this species. We needed to design a survey that enables population size to be estimated when density varies by several orders of magnitude and the number of animals present changes rapidly.

Materials and Methods

Study Area and Design

The survey design included three strata: (1) concentrations, i.e. whelping patches, (2) scattered pups in areas of historically high pup densities, and (3) scattered pups in areas of historically low densities. These historical distributions were derived from Canadian and Norwegian reports on sealing in Canadian waters and Canadian research surveys. Our surveys were designed to have a high probability of detecting patches (which are generally >5 nmi (9.3 km) in width (Hay and Wakeham 1983b)) in areas of historically high density (Fig. 1). At the Front, transects through strata of historically low and high pup

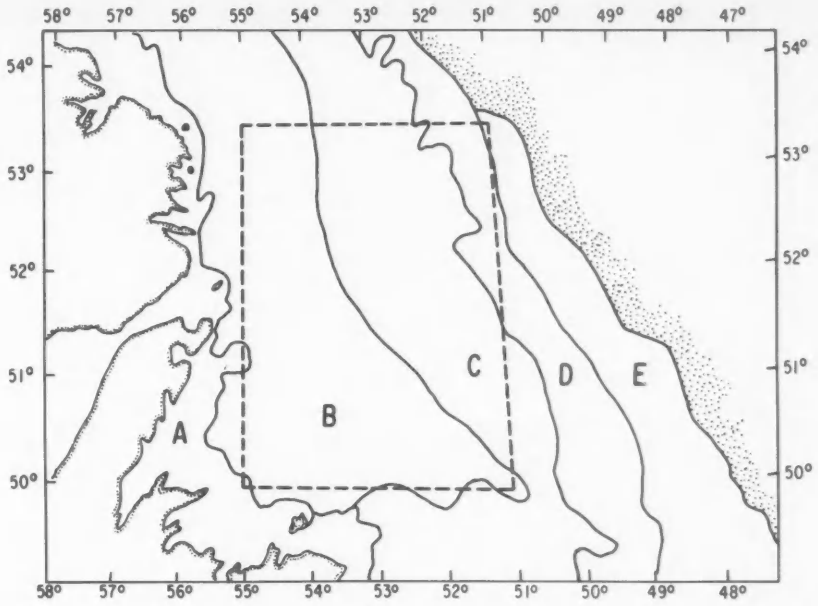

FIG. 3. Ice conditions off northeast Newfoundland and southeast Labrador on 20 March 1984 (Atmospheric Environment Service, Ottawa, Ont.). The study area is shown as a broken box (A, shore-fast ice; B, 90% coverage by 30–70 cm of ice; C, 90%+ coverage by 70–120 cm of ice; D, 60% coverage by 30–70 cm of ice; E, 20% coverage by 30–70 cm of ice). The stippled area indicates open water.

density were flown at intervals of 10 and 6 nmi (18.5 and 9.3 km), respectively (Fig. 2). The area surveyed covered ice conditions that appeared to represent suitable pupping habitat in 1984 (Fig. 3). In the Davis Strait, historical records were not as extensive (Fig. 4). For this reason and because of the long transit time from the survey base (Søndre Strømfjord), a 15-nmi (28-km) interval was used between transects in the Davis Strait study area. Two days were required to cover the study area at each location.

The overall design was to use fixed-wing aircraft to locate pupping concentrations during the course of flying the regularly spaced search transects described above. Photographs were taken along these search transects to enable the estimation of pup production in strata 2 and 3. Once located, concentrations (stratum 1) were surveyed using both fixed-wing aircraft (photographic) and helicopters (sighting) to estimate pup numbers on the ice and to obtain additional information used to estimate the distribution of births over time.

Fixed-Wing Surveys

A Piper Navajo PA-31 (a low-wing, twin-engine aircraft with a range of about 7 h) was used for the photographic surveys. Altitude (305 m over the Front and 305 or 335 m over Davis Strait) was controlled using a radar altimeter. The aircraft was equipped with a VLF-Omega navigation system. Vertical photographs (23 × 23 cm) were taken using a Wild RC-8 camera equipped with a Universal lens (calibrated focal length of 151.997 mm at the Front and 152.287 mm at Davis Strait) and Kodak Double-X aerographic black and white film (type 2405).

In Davis Strait, transects extended from the ice edge to well inside the heavy pack ice to the west, whereas at the Front, transects extended from the heavy coastal ice to the seaward edge of the heavy pack ice (Fig. 2 and 3). To estimate the density of scattered pups, spot-photographs were taken along each transect at an interval of 3.5 km at the Front and 6.4 km in Davis Strait.

A single concentration of whelping hooded seals was found in each study area (Fig. 2 and 4). Along each transect within the concentration a continuous strip survey was conducted and an intervalometer was used to obtain 15–20% overlap between successive photographs. The first photo-transect was flown along one edge of the patch; subsequent transects were spaced uniformly (about 4 km apart) to ensure accurate navigation and complete coverage of the patch. The photographic survey was terminated when no seals were seen on two adjacent transects. Transects began and ended a short distance outside the concentration, but the photographic sequence began only when seals were first seen along the transect and ended when seals were no longer seen. The position of the aircraft was recorded at the beginning and end of the photographic sequence. Radiotransmitters (frequency 148.50–148.95 MHz; range ≈30 km; Telonics, Mesa, Arizona) were deployed at both concentrations to facilitate relocation.

The number of pups with and without their mothers was recorded from black and white prints (23 × 23 cm) of the photographs. Each print was examined once either with a binocular microscope under 12× magnification or with an illuminated hand-lens of magnification 7–8×. A 64-cell acetate grid was overlain on photographs to improve counting accuracy.

Helicopter Surveys

During sighting surveys with a Hughes 500D helicopter,

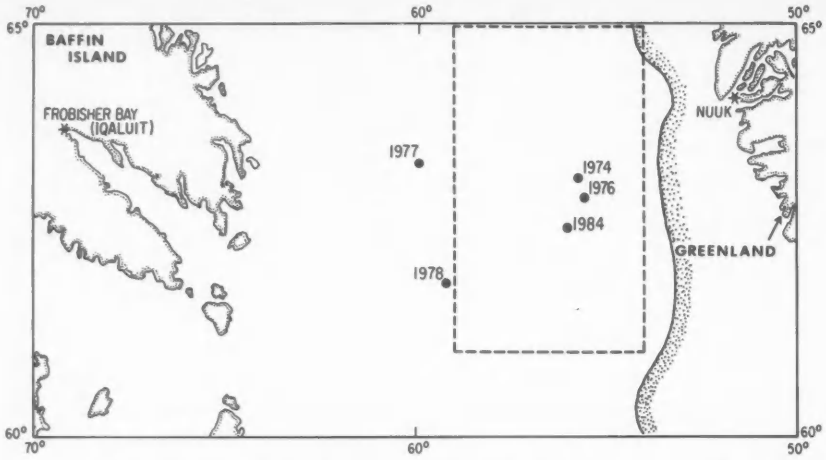

FIG. 4. Distribution of whelping concentrations of hooded seals in Davis Strait in 1974, 1976–78, and 1984 (Sergeant 1974, 1976, 1977; MacLaren Atlantic Ltd. 1977; MacLaren Marex, Inc. 1979). The broken box represents the 1984 study area. The approximate position of the ice edge on 22 March 1984 (with open water to the eastward) is indicated by a solid line with adjacent stippling.

each observer (one port rear, one starboard rear) scanned a strip 100 m wide. Observers calibrated their strips by placing reference marks on the window using as reference a series of dye marks on the ice spaced at 100-m intervals. Altitude for the helicopter surveys was maintained at 30.5 m using a barometric altimeter which was frequently adjusted at ice level for changes in pressure. Helicopter ground speed was about 150 km/h for Davis Strait and 110–170 km/h for the Front surveys.

The first transect of helicopter surveys was positioned along one edge of the patch and subsequent parallel transects were spaced at intervals of 1.85 km. Each transect was terminated when no seals were seen over a distance of about 2 km along it. The survey ended when no seals were seen along two consecutive transects. At the Front, beginning and ending positions of each line were recorded from a Loran-C navigation unit. In Davis Strait, the surveys were done by dead reckoning and the pilot adjusted indicated airspeed and heading for wind direction and speed to give a true ground speed of about 150 km/h and to ensure that all transects were oriented north–south.

Duration of Pup Stages

Hooded seal pups were classified into four readily identifiable developmental stages based on observations of pups in March 1983.

Stage 1: Newborn — skin in loose folds along flanks, fur saturated to wet, entire pelage with yellowish hue, awkward body movements. Mother present.

Stage 2: Thin blueback — ventrum white, neck well defined, trunk conical in shape. Mother present.

Stage 3: Fat blueback — ventrum white, neck not clearly distinguishable, trunk fusiform in shape. Mother present.

Stage 4: Solitary blueback — as in fat blueback but mother not present.

We are confident that pup stages 3 and 4 can be distinguished reliably based on the presence or absence of the mother. Bowen et al. (1985) found no instance of a pup without its mother that had milk in its stomach or showed other indications of suckling such as weight gain.

To determine the duration of each stage, we followed the development of known-age individuals from birth to weaning and beyond. Pups were marked with Dalton Rototags to which were attached vinyl-cloth streamers (3 × 20 cm) to enable rapid identification from the air. Dye of various colors (Day Glo series Z) was also applied to both pups and adjacent ice to facilitate relocation. Known-age individuals were located daily or more frequently as time and weather permitted and classified into one of the above four stages.

Statistical Methods

Estimates of pup numbers on the ice during each survey

We estimated the number of scattered seals (those outside the whelping patches) by multiplying the area surveyed by the average density of seals determined from spot-photographs. Confidence limits for the density estimates were obtained by a bootstrap resampling procedure (Efron 1979).

The total and standard error of the number of pups present on the ice in whelping concentrations were estimated using the strip survey method for unequal-sized sampling units (Caughley 1977, p. 31). The area of each concentration was determined by connecting transect end-points and adding a strip 0.5 nmi (0.93 km) wide beyond the beginning and ending transects.

Estimation of total pup production in whelping concentrations

In this section we outline a method for estimating total pup production in a whelping concentration using estimates of the numbers of pups on the ice at several times and an estimate of the distribution of births over time derived from changes in the proportion of pups in different developmental stages. This method is similar to a method for analyzing catch-at-age data by Fournier and Archibald (1982); we have used their notation where possible.

We assume that the rate at which pups are born can be adequately approximated by a continuous function of time, $m_1(t)$, and that pups pass through a series of identifiable stages,

TABLE 1. Developmental stage of 49 known-age hooded seal pups at the Front in relation to age.

Days postpartum	Developmental stage				
	Newborn	Thin blueback	Fat blueback	Solitary	Total
1	0	34	4	0	38
2	0	4	36	0	40
3	0	1	19	6	26
4	0	0	4	10	14
5	0	0	0	4	4
6+	0	0	0	6	6
Total	0	39	63	26	128

the durations of which vary from pup to pup. Stages are denoted by the subscript j. We specify stage duration in terms of instantaneous transition intensity functions

$$\phi_j(\tau) = \lim_{\Delta\tau \to 0} \{\text{Probability an animal passes from stage } j \text{ to } j+1 \text{ in the interval } (\tau, \tau+\Delta\tau)\}/\Delta\tau$$

where τ is the time spent in the stage j. Thus, the probability of a seal passing to the next stage depends only on the time spent in the preceding stage, i.e. it is assumed to be a semi-Markov process. Note that $\phi_j(\tau)$ is defined only for positive τ and its complete integral is 1. This specifies how the transition probabilities into stage $j+1$ from stage j change with the amount of time, τ, that an animal has spent in stage j. A similar development for an insect population is given in Ashford et al. (1970).

The rate at which individuals enter stage j at time t is denoted by $m_j(t)$. Since mortality is negligible for hooded seal pups during their period on the ice, the m_j's are connected by the recurrence relationship

$$(1) \quad m_j(t) = \int_0^\infty m_{j-1}(t-\tau)\, \phi_{j-1}(\tau)\, d\tau.$$

The number of individuals in stage j at time t, $n_j(t, \boldsymbol{\theta})$, is

$$(2) \quad n_j(t, \boldsymbol{\theta}) = \int_0^\infty m_j(t-\tau) \left(1 - \int_0^\tau \phi_j(s)ds\right) d\tau$$

where $\boldsymbol{\theta}$ is a vector of parameters describing $m_1, \phi_1, \phi_2, \ldots$.

Suppose that a number of times t_i, $i = 1, \ldots, N$, a number of animals are classified into stages. Let S_{ij} be the number of individuals observed to be of stage j at time t_i. Let O_l be the estimated total number of individuals at time t_l, C_l be the actual number at time t_l, and P_{ij} be the actual proportions of individuals of stage j at time t_i.

Errors in estimating pup abundance using the aerial strip surveys are assumed to be normal (Caughley 1977). That is,

$$(3) \quad O_l = C_l + \epsilon_l$$

where the ϵ_l's are independent normally distributed random variables with mean 0 and variance σ_l^2. The error variances of the strip survey are estimated from the data as described by Caughley (1977).

The assumption that the errors in estimating pup abundance are normal was made because the biases inherent in confidence regions constructed using the normal approximation are known and produce conservative estimates in the sense that the estimated lower and upper limits of the 95% confidence interval will be less than that derived using the correct, right-skewed error distribution. This assumption introduces a negative bias in our estimates of total pup production. This bias is preferable to the unknown, possibly positive, bias introduced by a logarithmic transformation when the conservation of a population is the prime concern. A more reasonable model assumption is not possible with the data available to us.

The samples used to determine stage classes were cluster samples taken from whelping concentrations in which there was significant spatial variation in the proportion of pups in each stage. Thus the effective sample size S_{ij}' must be estimated. If samples of equal size B were taken from each cluster, then

$$(4) \quad S_{ij}' = \alpha_i S_{ij}$$

where

$$\alpha_i = \frac{1}{1 + \rho_i (B-1)}$$

where ρ_i is intraclass correlation at time t_i calculated by assigning stages numerical values 1, 2, 3, and 4 and where B is the mean subsample size (Kish 1965). In the case where subsample size is not equal, then B is usually adequately approximated by the mean size of the cluster samples (Kish 1965).

Given the above stochastic assumptions, it follows that the likelihood function

$$(5) \quad L(\boldsymbol{\theta}) \propto \prod_{ij} P_{ij}^{\alpha_i S_{ij}} \prod_l \frac{1}{\sqrt{2\pi}\sigma_l} \exp\left(-\frac{1}{2}\left(\frac{O_l - C_l}{\sigma_l}\right)^2\right)$$

where the proportions P_{ij} are calculated as

$$P_{ij} = \frac{n_j(t_i, \boldsymbol{\theta})}{\sum_j n_j(t_i, \boldsymbol{\theta})}$$

where the $n_j(t_i, \boldsymbol{\theta})$'s are given by equation (2). The C_l's are determined similarly, i.e.

$$C_l = \sum_j n_j(t_l, \boldsymbol{\theta}).$$

It is not possible to estimate all of the parameters in $\boldsymbol{\theta}$ describing $m_1, \phi_1, \phi_2, \ldots$ using the likelihood function (5). We estimate the parameters in the transition intensity functions, ϕ_j, for the first three stages from independent data on known age pups (Table 1).

The transition intensities ϕ_2 and ϕ_3 were assumed to have gamma distributions. Let the proportion of the known-age population in stage j ($j = 2, 3, 4$) i days after the end of stage 1 be q_{ij}. For any particular parameter values of the gamma distribution the proportion q_{ij} can be calculated by setting m_1 to 1 at time zero and iterating equations (1) and (2). The likelihood of any combination of parameters is proportional to

$$\prod_{i=1}^{6} q_{i2}^{N_{i2}}\, q_{i3}^{N_{i3}}\, q_{i4}^{N_{i4}}$$

where N_{ij} is the observed number of known-age pups in stage j, i days after the end of stage 1. As cluster samples were not used here, the factor α_i (equation (4)) is not needed. The above equation does not allow us to estimate the duration of the solitary stage (stage 4). Thus, we will estimate the duration of this stage from the observed survey data, not the data on known age pups. We assume a simplified form for $\phi_4(\tau)$, i.e. that all pups leave stage 4 after a duration of time d_4.

Initially the distribution of births over time was assumed to be normal, with a mean date of birth (μ_b), variance in birth date (σ_b^2), and total number of pups born (N). A gamma distribution

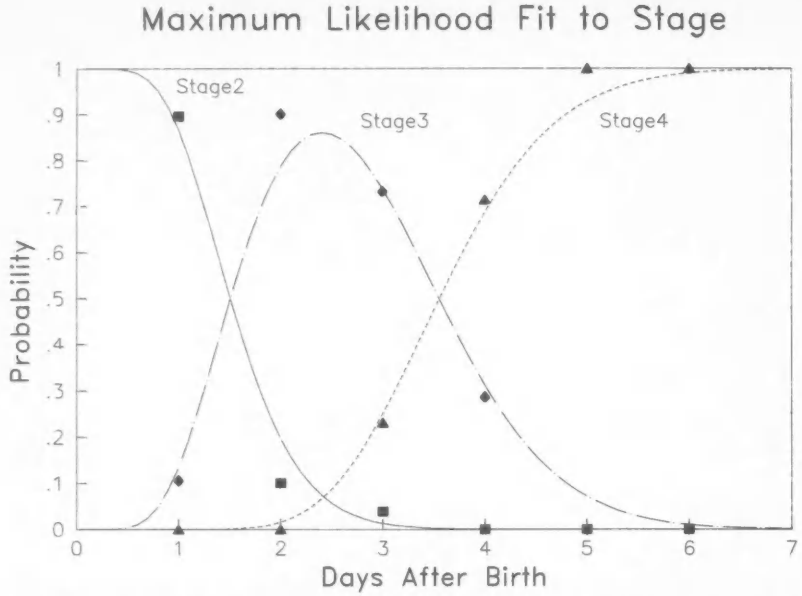

FIG. 5. Observed proportions and maximum likelihood estimates of the probability of a pup being identified as belonging to stage 2 (■, observed; —, fit), stage 3 (◆, observed; ---, fit), and stage 4 (▲, observed; ·—·, fit) as a function of known age.

was also investigated as a suitable form for $m_1(t.)$ That is,

$$(6)\quad m_1(t) = \frac{N(t-\eta)^{\kappa-1}\exp[-(t-\eta)/\theta]}{\theta^{\kappa}\Gamma(\kappa)}$$

where $\Gamma(\kappa)$ is the gamma function and η, θ, and κ are location, scale, and shape parameters, respectively. One more parameter must be estimated for the gamma distribution than for the normal.

Approximate confidence regions can be constructed using the likelihood ratio test (Cox and Hinkley 1974). Let the vector of parameters be $\boldsymbol{\theta}$, with dimension d, and let the maximum likelihood estimate of $\boldsymbol{\theta}$ be $\hat{\boldsymbol{\theta}}$. The approximate $1 - \alpha$ confidence region for $\boldsymbol{\theta}$ is the set of values $\boldsymbol{\theta}^*$ such that

$$(7)\quad \log L(\hat{\boldsymbol{\theta}}) - \log L(\hat{\boldsymbol{\theta}}^*) \leq \tfrac{1}{2}c^*_{d,\alpha}$$

where $c^*_{d,\alpha}$ is the upper α point of the chi-squared distribution with d degrees of freedom (Cox and Hinkley 1974). The above approach is preferable to the more commonly used method that relies on the asymptotic normal distribution because the certainty of estimates of population size are rarely symmetric.

The maximization of the likelihood function (5) is a nontrivial problem. We used two methods to maximize the likelihood, the Nelder–Mead simplex algorithm (which should not be confused with the linear-programming simplex algorithm) and a quasi-Newton algorithm that uses numerically calculated first and second derivatives of the log-likelihood function available as the IMSL routine ZXMIN (both of these methods are discussed in Bard 1974). We found the Nelder–Mead algorithm to be more reliable because it was less susceptible to round-off errors in calculating the log-likelihood function. The calculation of the integrals in equations (1) and (2) must be performed numerically. Details of the implementation and program listings can be obtained from Ransom A. Myers.

Results

Duration of Pup Stages

On 18 and 19 March at the Front, 62 newborn pups were individually marked. A total of 128 resightings were made on 49 of these known-age seals (Table 1). All pups initially classified as newborn were reclassified as thin bluebacks at 1 d of age. We had insufficient information to estimate the duration of the first stage. However, observations of newborn harp (*Phoca groenlandica*) and grey seals (*Halichoerus grypus*) suggest that hooded seal pups would be judged as newborns for approximately 3 h (Brian Beck, Department of Fisheries and Oceans, Dartmouth, N.S., pers. comm.). It is clear from Table 1 that there is considerable individual variation in stage duration. Weaning occurred by 3 d postpartum in 6 of 26 seals and by 4 d postpartum in 10 of 14 seals. According to Bowen et al. (1985), pups are usually weaned at 4 d after birth. The number of pup resightings declined over time as a result of reduced visibility during fog, breakup and shifting of ice, and dispersal of solitary pups. Therefore, the length of time solitary pups remain on the ice cannot be estimated from Table 1.

Because our observations were relatively widely spaced in time, it did not seem justified to fit two independent gamma distributions for stages 2 and 3 to the data in Table 1. We made the assumption that the shape of the transition intensity function was the same for stages 2 and 3, but that the scale parameter was different for each of the two stages. The resulting estimates of the scale parameter are 0.18 for the thin blueback stage and 0.24 for the fat blueback stage with a common shape parameter $\kappa = 0.86$. The fit to the data was good (Fig. 5). The three-parameter model was identified, i.e. the correlations between the estimates were all less than 0.75. A four-parameter model, separate κ's for each stage, was not justified given that the ratio

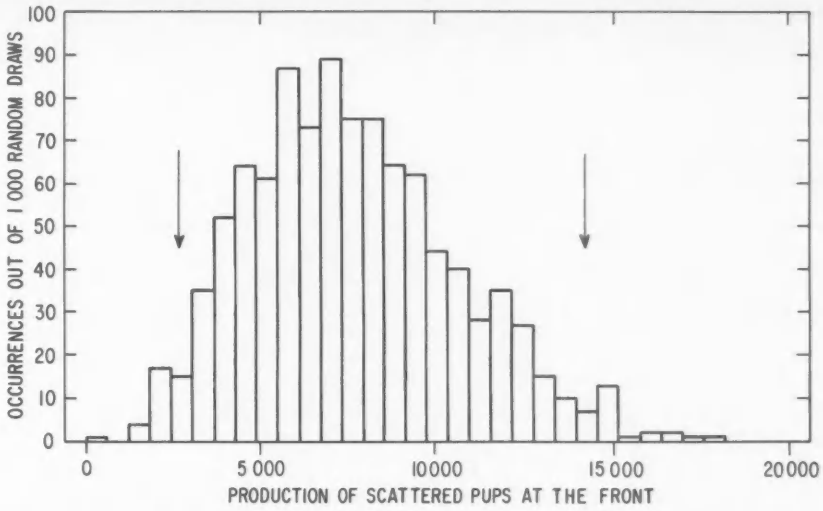

FIG. 6. Histogram of 1000 bootstrap simulations of the data on scattered seals at the Front. The 95 percentile limits are indicated by arrows.

of the maximum log-likelihood of the four- and three-parameter models was less than 2 (Kendall and Stuart 1979).

Estimation of Pup Production

"Scattered" pups at the front

Twelve hooded seal pups were seen on the 472 spot-photographs in the area with historically high densities of pups (Fig. 1 and 2), giving an estimate of 0.12 pups/km^2 over 61 138 km^2 or a total of 7400 scattered pups on the ice. The 95% confidence limits for this estimate are 2700 to 14 400 (Fig. 6).

Although there is a substantial gap in aerial coverage of this stratum, we felt that extrapolation of the estimated density to the entire area of the high-density stratum is justified, given the homogeneity of the ice conditions (Fig. 2 and 3).

The bootstrap confidence limits were checked using a parametric method. The scattered seal pups are clearly not randomly distributed; one of the photographs showed four pups. The negative binomial distribution provided a significantly better fit to the data than a Poisson distribution (log-likelihood test, $P < 0.05$). The maximum likelihood estimate of the mean density of the negative binomial distribution is the observed mean; the estimate of the negative binomial k parameter was 0.0283. The 95% confidence interval for the number of scattered pups based on plots of the log-likelihood contour surface of the mean and k (using equation (7)) is from 2300 to 31 000. The likelihood-based confidence limits are larger because two parameters are being estimated (the mean and k), with a concomitant loss of precision. The bootstrap confidence limits seem preferable here because they require no parametric assumptions and do not require a nuisance parameter to be estimated.

Front concentration

Photographic surveys of the hooded seal concentration at the Front were flown on 20, 21, and 25 March (Fig. 2). None of these photographic surveys covered the entire concentration because of poor weather (see Hay et al. 1985 for details); however, information on the proportion of solitary pups in these surveys was used.

The results of complete helicopter surveys of the concentration on 21 and 25 March are shown in Tables 2 and 3. The peak abundance of hooded seal pups on the ice was 35 260 (95% confidence interval of 24 940 to 45 590) on 21 March, with a mean density of 56 pups/km^2. By 25 March the number of pups on the ice in the concentration had declined to 24 020 (95% confidence interval of 18 860 to 29 170), with a mean density of 47 pups/km^2.

An alternative method of calculating the confidence limits, suggested by a referee, is to use a ratio estimator in which the number of seal pups seen per transect is related to transect length (Cochran 1977, chap. 6). The resulting 95% confidence limits calculated using the data in Tables 2 and 3 and formula 6.9 in Cochran (1977) are 32 387 to 38 177 for 21 March 1984 and 22 944 to 25 143 for 24 March 1984. These confidence intervals are smaller than those obtained using Caugley's method, and are probably unreliable because the variance estimator for the ratio method is severely negatively biased for sample sizes less than 30 (Cochran 1977).

Initial estimates of the total numbers of pups born in the patch were made assuming that the distribution of births over time was normal and that the time solitary pups remain on the ice, d_4, was constant and the same for all pups. Equation (4) was used to reduce the effective sample size of the stage proportion data because simple random sampling was not achieved (Table 4). Estimates of the effective sample size were lower than the number actually observed because of the positive intraclass correlation coefficient. The estimate of total pup production (55 000) indicates that a significant correction is needed to account for pups that had already left the ice or were yet to be born on 21 March when the maximum number of pups was observed (Table 5). The estimate of peak pupping, 17 March, is consistent with the qualitative estimates made by researchers on the ice. Two-dimensional slices of the 95% confidence region provide a better indication of the precision of the estimates than do confidence intervals (Fig. 7). The largest correlation among the parameter estimates was between N and

TABLE 2. Summary of pelage stage counts from the complete helicopter survey of hooded seals carried out at the Front on 21 March 1984 (patch area = 636 km^2; maximum number of transects = 120; survey altitude = 30.5 m; strip width = 0.2 km; sampling intensity = 10.7%).

Transect No.	No. of hooded seal pups counted					Transect length (km)	Density of pups (no./km^2)
	Newborn	Thin blueback	Fat blueback	Solitary	Total		
1	1	14	326	331	672	28.2	119.1
2	0	15	252	346	613	31.9	96.1
3	1	9	160	179	349	33.1	52.7
4	0	7	91	170	268	29.8	45.0
5	0	1	63	142	206	23.1	44.6
6	0	1	14	60	75	12.9	29.1
7	0	6	215	177	398	34.5	57.7
8	0	21	180	71	272	34.5	39.4
9	0	3	60	90	153	27.6	27.7
10	0	9	91	64	164	25.8	31.8
11	0	13	105	53	171	25.2	33.9
12	3	17	151	63	234	17.3	67.6
13	2	17	127	38	184	14.9	61.7
Total	7	133	1835	1784	3759	338.8	

TABLE 3. Summary of pelage stage counts from the complete helicopter survey of hooded seals carried out at the Front on 25 March 1984 (patch area = 509 km^2; maximum number of transects = 222; survey altitude = 30.5 m; strip width = 0.2 km; sampling intensity = 10.8%).

Transect No.	No. of hooded seal pups counted					Transect length (km)	Density of pups (no./km^2)
	Newborn	Thin blueback	Fat blueback	Solitary	Total		
1	0	0	11	3	14	8.3	8.4
2	0	0	13	13	26	9.7	13.4
3	0	1	42	32	75	10.2	36.8
4	2	5	73	45	125	10.0	62.5
5	0	7	56	44	107	10.0	53.5
6	0	2	23	55	80	10.5	38.1
7	0	14	97	32	143	11.2	63.8
8	0	4	49	46	99	10.2	48.5
9	0	7	86	53	146	10.5	69.5
10	0	7	77	31	115	13.8	41.7
11	0	2	55	52	109	13.8	39.5
12	0	5	26	52	83	13.8	30.1
13	0	1	6	63	70	13.0	26.9
14	0	0	11	163	174	10.7	81.3
15	0	1	24	134	159	14.3	55.6
16	0	1	37	101	139	14.8	47.0
17	0	2	12	85	99	11.6	42.7
18	0	0	5	174	179	9.2	97.3
19	0	2	9	186	197	10.0	98.5
20	1	1	8	239	249	12.5	99.6
21	0	1	3	55	59	9.4	31.4
22	0	0	2	39	41	9.4	21.8
23	0	1	0	63	64	17.0	18.8
24	0	0	0	46	46	11.2	20.5
Total	3	64	725	1806	2598	275.1	

TABLE 4. Observations used in the likelihood function for estimation of total pups born in the Front patch. Only partial data are available for 20 March. (S_{i1}, S_{i2}, S_{i3}, and S_{i4} = number of pups counted in stages 1 through 4, respectively, O_i = estimated number of pups on the ice from surveys, σ_i = standard deviation of O_i, ρ_i = intraclass correlation coefficient at time i, and α_i = effective sample size correction coefficient)

Date	S_{i1}	S_{i2}	S_{i3}	S_{i4}	O_i	σ_i	ρ_i	α_i
20 March	(	655	)	476	—	—	0.057	0.071
21 March	7	133	1835	1784	35 264	4735	0.13	0.027
25 March	3	64	725	1806	24 017	2490	0.29	0.03

d_4 (Fig. 7C). Thus, the precision of the estimates would be greatly improved if an independent estimate of the duration of the solitary stage, d_4, was available.

The largest residuals from the model fit are the numbers in stages 1 and 2 on 21 March which were underestimated (Fig. 8). This discrepancy is probably due to model error, i.e. the distribution of births may not be unimodal as assumed and a pulse of births may have occurred between the surveys of 21 and 25 March.

It is important to give proper weight to each part of the likelihood function. For example, if the correction factor α_i in equation (4) was set equal to 1, the results would be unreliable because too little weight is given to the point estimates of total abundance.

The sensitivity of the estimates to the functional form of $m_1(t)$ was investigated by assuming that the distribution of births over time followed a gamma distribution (Table 5; equation (5)). The pup production estimate was similar to that obtained from the model assuming a normal distribution for m_1 ($N \simeq 48\,000$ pups); however, this estimate is not reliable because the gamma model was not identified, i.e. the parameter estimates were highly correlated.

From the data available, it is not possible to fit a more complex model for the shape of the distribution of births over time. It is possible to examine the effect of a nonsymmetric distribution by truncating the left tail of the normal distribution at various early dates. Pupping could have begun no later than 13 March because stage 2 pups were present when the concentration was first found on 16 March. So 13 March is the latest date at which we can experimentally truncate the birthdate distribution. If we do so, then the estimate of pup production goes down by 16%. In future aerial surveys, earlier estimates of pup stage composition would reduce this uncertainty.

The assumption that the duration of the solitary stage is constant is clearly an approximation. Although we do not have sufficient data to include an analysis of a variable stage 4 duration, an analysis of a much more extensive data set on harp seals showed that the variability of the last stage had little effect on the estimate (Myers and Bowen 1986).

Davis Strait patch

On the spot-photographs taken in Davis Strait, no pups were seen which could unambiguously be attributed to production outside of the whelping concentration (pups further than about 18.5 km from the patch). Therefore, we make no estimate of the abundance of scattered pups in this region.

Prior to 24 March the ice in Davis Strait was tightly packed with few openings so that at the time of the 24 March helicopter survey, few seals (pups or their mothers) could have left the

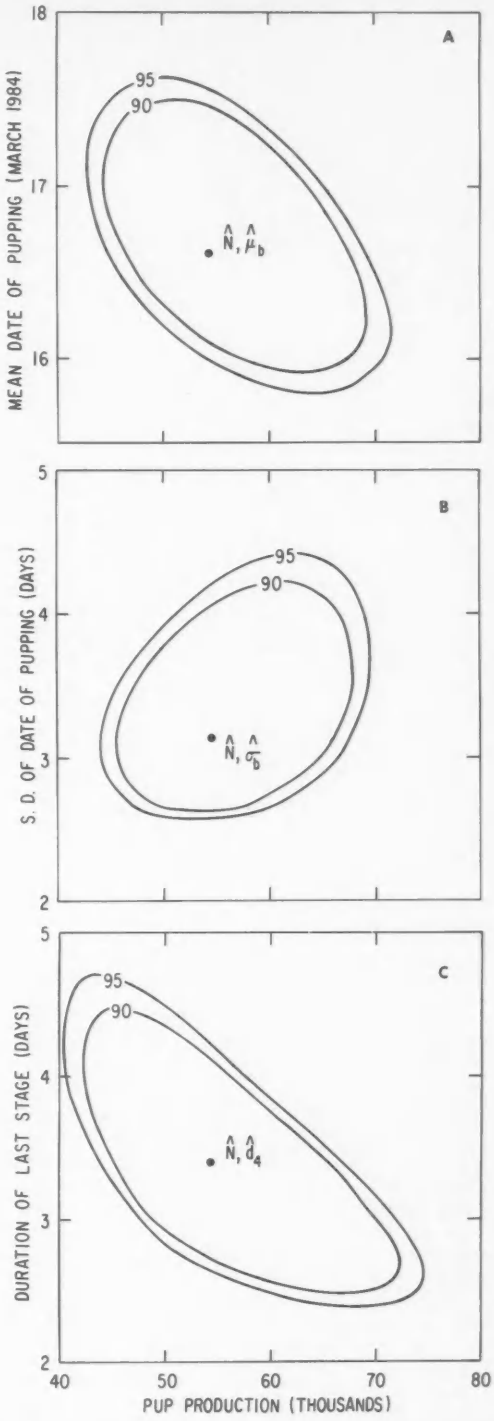

FIG. 7. Two-dimensional slices of the 95% joint confidence region for trial 1 in Table 5, calculated using the log-likelihood ratio.

TABLE 5. Parameter estimates and 95% confidence limits calculated from equations (5) and (7) (N = total pup production, μ_b = mean birthdate, σ_b = standard deviation of mean birthdate, and d_4 = duration of solitary stage on the ice).

Trial	Birthing distribution assumed	N	Birthing distribution estimates	d_4 (d)	Maximum log-likelihood
1	Normal	55 000 (41 000 to 75 000)	μ_b = 16.6 (15.8–17.6) σ_b = 3.14 (2.55–4.4)	3.4 (2.4–4.75)	207
2	Gamma	48 200 ± 13 930	κ = 8.89 ± 31.4 θ = 1.0 ± 1.74 η = 8.78 ± 17.0	3.57 ± 1.0	206

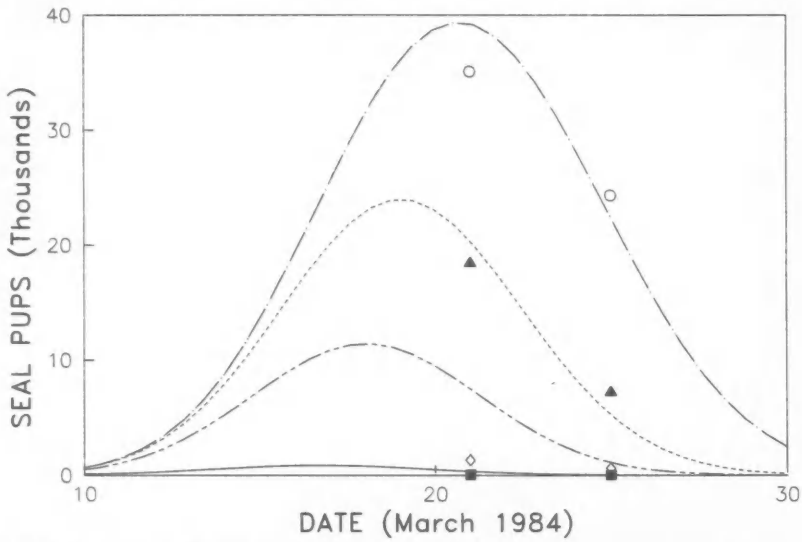

FIG. 8. Observed and estimated proportions of the pups of different stages present on the ice off Labrador in 1984, using the assumption of a normal birthing distribution (trial 1, Table 5): observed (■) and estimated (—) stage 1 pups, observed (◇) and estimated (--) stage 1 and 2 pups, observed (▲) and estimated (---) stage 1, 2, and 3 pups, and observed (○) and estimated (·—·) stage 1, 2, 3, and 4 pups.

ice. Because of these ice conditions, applying the model describing the distribution of births over time resulted in no correction to the 24 March helicopter estimate of numbers. It is unlikely that many pups would have been born after 24 March; therefore, we consider the 24 March survey to be our best estimate of the number of pups born in the Davis Strait concentration. This survey gave an estimate of 18 590 pups present on the ice, with a 95% confidence interval of 13 750 to 23 440 and a mean density of 21.8 pups/km^2 (Table 6).

A complete fixed-wing photographic survey of this concentration, flown on 25 March, gave an estimate of 9820 pups on the ice (95% confidence interval of 2630 to 17 020), with a mean density of 8.5 pups/km^2 (Table 7).

Discussion

There are three important conclusions arising from this study: (1) hooded seal pup production in the Northwest Atlantic is considerably greater than previously thought, (2) because of the short lactation period, the correction for the distribution of births over time is large and cannot be neglected if accurate population estimates are to be made, and (3) scattered pups outside the main concentrations may compromise a significant proportion of total production.

Our population estimates are probably underestimates of total production for three reasons. First, large concentrations of pups could have been missed within the study areas, although we have no evidence that this occurred. Second, the areas that contain ice suitable for pupping are larger than the areas surveyed. There could have been substantial numbers of scattered seals which could not be surveyed without an additional aircraft. Third, the estimate of the number of scattered pups was not corrected for pups that had left the ice or were yet to be born at the time the surveys were flown. We did not feel justified in extrapolating the distribution of births over time within the concentration to the areas of low density. Furthermore, in the

TABLE 6. Summary of sighting results from a complete helicopter survey of hooded seals carried out in the Davis Strait on 24 March 1984 (patch area = 852 km^2; maximum number of transects = 193; survey altitude = 30.5 m; strip width = 0.2 km; sampling intensity = 10.4%).

Transect No.	No. of hooded seal pups counted				Transect length (km)	Density of pups (no./km^2)
	Thin blueback	Fat blueback	Solitary	Total[a]		
1	0	5	43	50	27.2	9.2
2	0	19	77	96	29.6	16.2
3	1	82	146	239	37.0	32.3
4	0	70	183	256	30.8	41.6
5	2	70	133	209	25.5	41.0
6	4	65	99	169	18.2	46.5
7	0	50	27	79	12.4	31.8
8	0	37	51	8	17.3	25.5
9	0	55	119	175	31.5	27.8
10	0	27	94	123	35.8	17.2
11	0	8	34	46	22.9	10.0
12	1	9	64	74	24.5	15.1
13	0	0	61	61	20.4	15.0
14	0	1	77	78	17.0	23.0
15	0	11	80	92	22.7	20.3
16	0	2	40	42	19.8	10.6
17	0	22	21	43	20.4	10.6
18	0	4	7	11	11.3	4.9
19	0	2	4	6	12.6	2.4
20	0	1	0	1	7.4	0.7
Total	8	540	1360	1938	444.2	

[a]Total pups does not always equal the sum of pups classified as thin, fat, or solitary because some pups could not be classified.

TABLE 7. Summary of photographic transect results from a complete fixed-wing aerial survey of hooded seals carried out in Davis Strait on 25 March 1984 (patch area = 1153 km^2; maximum number of transects = 75; survey altitude = 335 m; strip width = 0.503 km; sampling intensity = 7.8%).

Transect No.	No. of hooded seal pups counted					Transect length (km)	Density of pups (no./km^2)
	Families[a]	Female - pup	Female - 2 pups	Single pup	Total pups		
1	1	0	0	19	20	22.7	1.8
2	3	5	0	100	108	30.3	7.1
3	5	18	2	176	203	30.2	13.4
4	14	116	2	169	303	34.5	17.5
5	8	24	0	60	92	31.0	5.9
6	0	7	0	33	40	30.0	2.6
Total	31	170	4	557	766	178.7	

[a]Adult male/mother/pup.

Davis Strait it was not possible to take spot-photographs until 25 March. At this late date, few pups would be expected still to be on the ice, and therefore, it is not surprising that we failed to find scattered pups in this area.

Previous estimates of pup production in the Davis Strait have ranged from 9000 to 25 000 (Sergeant 1974, 1976, 1977; MacLaren Atlantic Ltd. 1977; MacLaren Marex, Inc. 1979). This range is largely the result of variation in design and completeness of these surveys.

Our Davis Strait helicopter survey of 24 March produced an estimate of 18 590 pups present (mean density of 21.8 pups/km^2) whereas the fixed-wing photographic survey on the next day produced lower estimates (9820 pups with 8.5 pups/km^2). This change was likely caused by the rapid breakup of the ice in the whelping patch around midday of 24 March which enabled weaned pups to enter the water. Earlier, the pack ice consisted of very large unbroken sheets of up to 2 km in diameter. Weaned pups which were in the middle of these sheets, far from leads or cracks, would have had no opportunity to migrate from the area. Thus, we believe that the 24 March

survey is the most accurate estimate.

It is difficult to compare our Davis Strait results with those of the other workers because previous surveys made no attempt to estimate the abundance of scattered pups or to account for pups which had left the ice or were yet to be born. Thus, it is not possible to determine recent trends in pup production at Davis Strait.

Our estimate of 62 400 pups (95% confidence interval of 43 700 to 89 400) at the Front is similar to that derived from spot-photographs taken along transects in this area in 1985 (Hay et al. 1985). Limited aircraft time in 1985 resulted in an imprecise estimate of 61 400 pups (95% confidence limits of 16 500 to 119 500). An aerial photographic survey, conducted in March 1983 (Hay and Wakeham 1983a), was also incomplete. Hay and Wakeham (1983b) calculated Front pup production using a Leslie analysis of pup catches. The authors considered their estimates of 8000 to 16 000, from 1977 to 1982, to be negatively biased by an unknown extent and therefore of marginal value because of violation of model assumptions. Furthermore, this method did not account for the birth of scattered pups.

Previous estimates of hooded seal pup production (27 000 to 41 000 for the period 1966–71) in the Northwest Atlantic have all been based on the survival index method (Benjaminsen and Øritsland 1975; Sergeant 1976; Winters and Bergfløtdt 1978; Anonymous 1983). However, the confidence limits for these estimates are large because the estimates depend heavily on a single data point (the high 1966 catch of pups).

If we accept that production in the mid-1960s was approximately 30 000, then it would appear that the hooded seal population has increased in recent years. The same conclusion is reached whether we believe that this represents total Northwest Atlantic production or only Front production. The extent of intermixing between Davis Strait and Newfoundland seals is unknown and therefore it is not known whether age samples taken at Newfoundland can also be used to estimate Davis Strait pup production.

Our study shows that hooded seal pup production can be estimated using aerial survey methods corrected for the flux of pups in whelping concentrations. However, the estimation of abundance could be improved if better information was available on the distribution of births over time both within and between whelping patches.

There is a need for more statistical research on survey designs to estimate the abundance of dispersed populations in which density varies greatly. Our design used historical data to construct survey strata so that our limited resources could be better allocated to improve the chances of discovering pupping concentrations, while enabling the estimation of the number of pups born outside these concentrations. There are clear advantages to using different survey methods for different strata when densities vary over several orders of magnitude. This approach would seem to be appropriate for other ice breeding seals (e.g. harp seal) and may have other more wide range applications as well.

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References

ANONYMOUS. 1973. Report of meeting of scientific advisors to panel A. *In* Proc. Special Commission Meeting January 1973 and the 23rd Annual Meeting June 1973. ICNAF Ser. No. 3112.

1983. Report on the meeting of an ad hoc working group on assessment of harp and hooded seals in the northwest Atlantic. ICES Coop. Res. Rep. No. 121. ICES Headquarters, Copenhagen.

1985. Report of Standing Committee on Fishery Science, p. 11–18. *In* NAFO Scientific Council Reports, December 1985.

ASHFORD, J. R., K. L. Q. READ, AND G. G. VICKER. 1970. A system of stochastic models applicable to studies of animal population dynamics. J. Anim. Ecol. 39: 29–50.

BARD, Y. 1974. Nonlinear parameter estimation. Academic Press, New York, NY.

BENJAMINSEN, T., AND T. ØRITSLAND. 1975. Adjusted estimates of year-class survival and production with estimates of mortality for northwest Atlantic harp seals. ICNAF Res. Doc. 75/XI/3.

BOWEN, W. D., O. T. OFTEDAL, AND D. J. BONESS. 1985. Birth to weaning in four days: remarkable growth in the hooded seal, *Cystophora cristata*. Can. J. Zool. 63: 2841–2846.

BURNHAM, K. P., D. R. ANDERSON, AND J. L. LAAKE. 1980. Estimation of density from line transect sampling of biological populations. Wildl. Monogr. 72: 202 p.

CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, London.

COCHRAN, W. G. 1977. Sampling techniques. 3rd ed. John Wiley & Sons, New York, NY.

COX, D. R., AND D. V. HINKLEY. 1974. Theoretical statistics. Chapman and Hall, London.

DOI, T. 1974. Further development of whale sighting theory, p. 359–368. *In* W. E. Schevill [ed.] The whale problem: a status report. Harvard University Press, Cambridge, MA.

EFRON, B. 1979. Computing and theory of statistics: thinking the unthinkable. SIAM (Soc. Ind. Appl. Math) Rev. 21: 460–480.

FOURNIER, D., AND C. ARCHIBALD. 1982. A general theory for analyzing catch at age data. Can. J. Fish. Aquat. Sci. 39: 1195–1207.

GODDARD, J. 1969. Aerial census of black rhinoceros using stratified random sampling. East Afr. Wildl. J. 11: 135–149.

HAY, K., G. B. STENSON, D. WAKEHAM, AND R. A. MYERS. 1985. Estimation of pup production of hooded seals (*Cystophora cristata*) at Newfoundland during March 1985. Can. Atl. Fish. Sci. Adv. Comm. 85/96.

HAY, K., AND D. WAKEHAM. 1983a. Estimation of pup production of hooded seals (*cystophora cristata*) at Newfoundland during March 1983 using vertical aerial photography. Presented at International Workshop on the Biology and Population Dynamics of Hooded Seals, Bergen, Norway.

1983b. Use of catch and effort data to estimate the pup production of hooded seals (*Cystophora cristata*) at Newfoundland. NAFO SCR Doc. 83/51, Ser. No. N709: 12 p.

KENDALL, M., AND A. STUART. 1979. The advanced theory of statistics. Vol. 2: Inference and relationship. 4th ed. MacMillan, New York, NY. 748 p.

KISH, L. 1965. Survey sampling. John Wiley & Sons, New York, NY. 643 p.

MACLAREN ATLANTIC LTD. 1977. Report on the Davis Strait aerial survey 77-1. Arctic Petroleum Operators Association, Project No. 134.

MACLAREN MAREX, INC. 1979. Report on aerial surveys of marine mammals and birds in southern Davis Strait and eastern Hudson Strait in March, 1978. Arctic Petroleum Operators Association, Project No. 146.

MYERS, R. A., AND W. D. BOWEN. 1986. Analysis of the 1983 aerial survey

of harp seals at the Front: corrections for the birthing curve and counting error. CAFSAC Res. Doc. 86/7.

NORTON-GRIFFITHS, M. 1973. Counting the Serengeti migratory wildebeest using two-stage sampling. East Afr. Wildl. J. 11: 135–149.

1975a. Counting animals. Publ. No. 1. Serengeti Ecological Monitoring Programme, African Wildlife Leadership Foundation, Nairobi, Kenya.

1975b. The numbers and distribution of large mammals in Ruaha National Park, Tanzania. East Afr. Wildl. J. 13: 121–140.

ØRITSLAND, T., AND T. BENJAMINSEN. 1975. Additional data on the sex ratio, age composition and mortality of Newfoundland hooded seals, with an estimate of pup production and sustainable yield. ICNAF Res. Doc. 75/122.

RASMUSSEN, B. 1960. On the stock of hood seals in the northern Atlantic. Fisken Havet 1: 23 p. (Fish. Res. Board Can. Transl. Ser. No. 387. 29 p. typescript)

SERGEANT, D. E. 1974. A rediscovered whelping population of hooded seals *Cystophora cristata* Erxleben and its possible relationship to other populations. Polarforschung 44: 1–7.

1975. Comments on new estimates of production and sustainable yield of harp and hooded seals. ICNAF Res. Doc. 75/147, Ser. No. 3720.

1976. Research on hooded seals *Cystophora cristata* Erxleben in 1976. ICNAF Res. Doc. 76/126, Ser. No. 4012.

1977. Research on hooded seals in the western North Atlantic in 1977. ICNAF Res. Doc. 77/57, Ser. No. 5132.

1978. Results of tagging and branding of hooded seals, 1972–78. ICNAF Res. Doc. 78/86, Ser. No. 5302.

SINCLAIR, A. R. E. 1973. Population increases of the buffalo and wildebeest in the Serengeti. East Afr. Wildl. J. 11: 93–107.

SINIFF, D. B., AND R. O. SKOOG. 1964. Aerial censusing of caribou using stratified random sampling. J. Wildl. Manage. 28: 391–401.

WIIG, Ø., AND R. W. LIE. 1984. An analysis of the morphological relationships between the hooded seals (*Cystophora cristata*) of Newfoundland, the Denmark Strait, and Jan Mayen. J. Zool. 203: 227–240.

WINTERS, G. H., AND B. BERGFLØDT. 1978. Mortality and productivity of the Newfoundland hooded seal stock. ICNAF Res. Doc. 78/91, Ser. No. 5307: 5 p. (Revised)

Periphyton in Lakes of Different Trophy[1]

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Cattaneo, A. 1987. Periphyton in lakes of different trophy. Can J. Fish. Aquat. Sci. 44: 296–303.

In a study of 10 lakes in the Eastern Townships (Quebec) periphyton biomass correlated less well with total P (TP) concentration in the water than did phytoplankton biomass. The relationship with TP was improved somewhat when periphyton biomass was estimated as cell volume rather than as chlorophyll or organic material. When the community was divided among various groups according to taxa, life form, and size, only the biomasses of greens, filamentous algae, and algae exceeding 10 000 μm^3 were correlated with TP. The biomass of the smaller algae, which are more readily grazed by benthos, was about the same in all lakes whereas nuisance forms increased significantly with P enrichment. At more eutrophic sites, maximal periphyton biomasses were observed in midsummer, coinciding with peak recreational use of lakes, whereas at the other sites, maxima appeared earlier in the season.

Dans une étude de dix lacs des Cantons de l'Est (Québec), la biomasse du périphyton était moins en corrélation avec la concentration totale de P dans la colonne d'eau que la biomasse du phytoplancton. La relation avec le P total était quelque peu améliorée quand la biomasse du périphyton était calculée comme volume de cellules au lieu de chlorophylle ou de matières organiques. Quand la communauté était divisée en groupes selon le taxon, la forme vitale et la taille, seules les biomasses d'algues vertes, d'algues filamenteuses et d'algues de taille supérieure à 10 000 μm^3 étaient en corrélation avec le P total. La biomasse des petites algues, plus vulnérables à la consommation par le benthos, était environ la même dans tous les lacs tandis que la biomasse de formes nuisibles a nettement augmenté avec l'apport de P. Aux endroits plus eutrophes, on a observé des biomasses maximales de périphyton à la mi-été; ceci coïncide avec la période d'utilisation de pointe des lacs à des fins récréatives tandis qu'aux autres endroits, ces maxima sont apparus plus tôt au cours de la saison.

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Although the periphyton is much less studied than the phytoplankton, it can play an important role in both the economy and ecology of lakes. High periphyton biomass is apparent as green or brown scums on stones and sediments in the littoral zone, detracting from the appearance and recreational value of lakes. At the same time, periphyton is an important primary producer in the littoral zone (Cattaneo and Kalff 1980) and a readily available food for invertebrates (Soszka 1975) and, indirectly, for fish.

The responses to eutrophication of phytoplankton biomass (Dillon and Rigler 1974; Nicholls and Dillon 1978), taxonomic composition (Smith 1983), and size structure (Watson and Kalff 1981; Sprules and Knoechel 1985) have been successfully quantified. Analogous relations, presuming that periphyton is also P limited, likely exist for periphyton, if somewhat changed by the peculiarities of growing attached to a substrate. Indeed, in rivers and artificial channels, chlorophyll concentration on artificial substrates is correlated with orthophosphate concentration and current (Horner and Welch 1981; Krewer and Holm 1982), and in lakes it is claimed that high P concentration increases periphyton development (Ennis 1975; Evans and Stockner 1972). A large biomass of filamentous green algae has been observed in the Great Lakes in response to point-source eutrophication (Auer et al. 1982). However, the relationships between natural periphyton and total P (TP) have not yet been determined. Such relations would be useful in littoral zone management, for they would indicate to what extent P abatement can control nuisance growth without compromising a useful source of food.

The aim of this study was to determine the periphyton response to increased TP concentration. Since nuisance problems are related not only to the quantity of periphyton but also to its quality and seasonality, I measured periphyton biomass, taxonomic composition, and size structure from spring to late summer in a series of lakes in the Eastern Townships (Quebec) that differed greatly in TP concentration.

Methods

Thirteen sites in 10 lakes of the Eastern Townships were chosen to represent a large range of nutrient levels and morphometry (Table 1). The physico-chemical characteristics, phytoplankton (Pace 1984), zooplankton (Pace 1986), bacteria (Bird and Kalff 1984), and macrophytes (Chambers and Kalff 1985) of these lakes have been described. The sites were sampled every 2 wk from May to August 1982. Since periphyton is more noticeable near shore and since stony

[1]Contribution of the Lake Memphremagog Project, Limnology Research Centre.

TABLE 1. Some physical and chemical (E. Betzen, Department of Biology, University of Waterloo, Waterloo, Ont., pers. comm.) characteristics of the epilimnion of the lakes studied. All lakes are within a 30-km radius of Lake Memphremagog (76°16′W, 45°06′N).

Lake	Area (km^2)	Max. effective fetch (km)	$\bar{Z}$ (m)	T ($\mu g\text{-}L^{-1}$)	TN:TP	Secchi disk (m)	Reflectance (%)
Argent	1.0	0.9	4.6	12.8	22.2	2.5	71
Brome	14.5	3.3	5.8	19.4	12.6	2.6	76
Brompton	11.9	2.1	12.5	7.9	43.9	2.7	81
Bowker	2.3	1.1	24.0	4.2	53.4	6.4	86
Lovering	4.6	1.4	15.6	8.5	38.0	3.1	82
Magog	10.8	2.1	9.8	47.8	10.4	1.9	66
Massawippi	17.9	1.0	40.2	11.9	39.2	2.6	77
Memphremagog–Border	100.0	4.4	6.2	13.5	20.4	3.6	78
Memphremagog–MacPherson	100.0	1.8	44.3	11.1	32.6	3.8	83
Memphremagog–Newport	100.0	0.4	6.2	23.8	15.5	1.8	57
Memphremagog–Pender	100.0	4.1	6.2	21.9	17.2	2.3	64
Orford	1.3	1.0	17.9	5.7	40.9	5.1	84
Waterloo	1.5	1.0	2.9	72.2	11.3	0.9	37

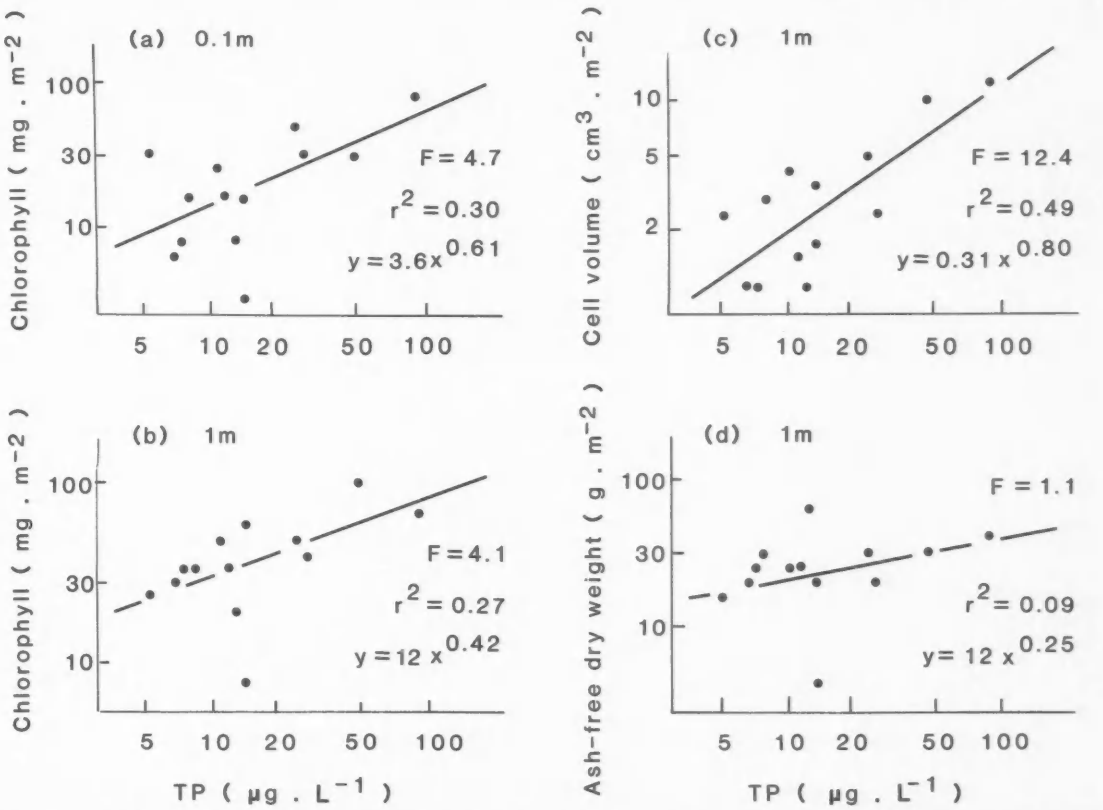

FIG. 1. Regressions between TP in the water and three indices of periphyton biomass. Data represent seasonal averages (26 May – 31 August 1982). Chl *a* was collected on stones at (a) 0.1 and (b) 1 m of depth, while (c) cell volume and (d) organic material were measured on stones at 1 m only. $P < 0.01$ for the regression between TP and cell volume, while the other relationships are not significant.

shores rarely extended deep into the lakes, stones were sampled at depths of 0.1 and 1 m. A brush-syringe sampler (Loeb 1981) was used to scrape, underwater, a constant area (5.7 cm^2) of randomly selected stones that varied in diameter from approximately 5 to 50 cm. To minimize the effect of very uneven periphyton distribution, scrapings from three stones were pooled for each sample and three such samples were collected at each depth (average CV = 28%).

Periphyton chlorophyll *a* (Chl *a*), corrected for pheophytin (Strickland and Parsons 1972), was determined by filtering an

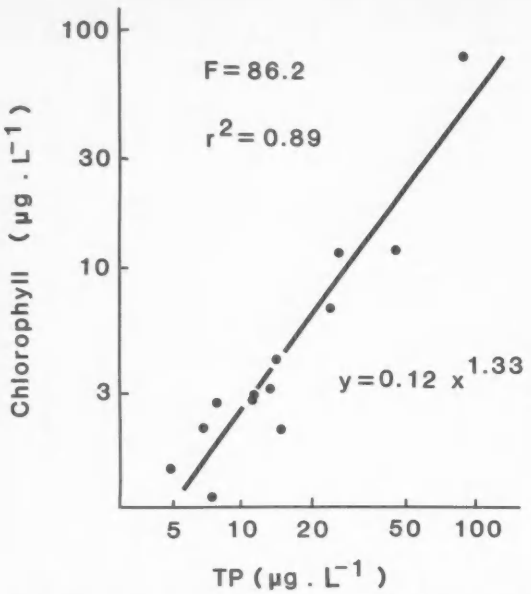

FIG. 2. Regression between TP in the water and Chl *a* of littoral phytoplankton in lakes of the Eastern Townships. Data represent seasonal averages (26 May – 31 August 1982).

aliquot of each pooled sample through Gelman type A-E glass-fibre filters. Filters were frozen and subsequently ground in 90% acetone. The extracts were read before and after acidification in a model 100 Bausch and Lomb spectrophotometer. Dry weight and ash-free dry weight were determined monthly, using a second aliquot of the 1-m sample. To determine dry weight, this aliquot was concentrated by centrifugation, dried at 60°C for 48 h, and weighed. Next, the sample was ignited at 550°C for 1 h and reweighed to determine the ash weight. Ash-free dry weight was calculated as the difference between these weights.

Aliquots collected at the first (late May), middle (mid-July), and last (late August) samplings were fixed with Lugol's iodine and subsequently used for examining the taxonomic composition of the communities. The algae were counted with an inverted microscope in random fields at 400× and 100× magnification. Large, rare algae were counted in the entire slide. Algae were classified by taxa, by life form (single cell, filament, colony), and by size. Cell volumes were calculated by approximation to solids of known volume. When colonies or filaments were present, the whole volume was taken as algal size rather than the volume of the single cell.

At each sampling, temperature, TP concentration in the water, and phytoplankton Chl *a*, also corrected for pheophytin (Strickland and Parsons 1972), were determined in an unfiltered subsurface water sample, collected near the 1-m-sampled stones. Analyses for TP employed the ascorbic acid modification of the molybdenum blue technique (Strickland and Parsons 1972) preceded by digestion under pressure with potassium persulfate (Menzel and Corwin 1965). Since Secchi disk transparency cannot be measured in shallow water, a closely correlated parameter, reflectance (Bergman and Peters 1980; Peters and Bergman 1986), was also determined in the water sample: 250 mL was filtered through a 0.45-µm-membrane filter and light reflected from the filter's surface was measured photometrically. The reduction in reflected light relative to an unused filter was used as a measure of sestonic pigment concentration.

The data were analysed using simple and multiple regression techniques (Statistix) on an IBM-PC. Prior to regression the data were logarithmically transformed to stabilize the variance.

Results and Discussion

Biomass

Chl *a*, organic material (ash-free dry weight), and cell volume were used to measure periphyton biomass. When the seasonal averages of these variables were regressed against TP, only cell volume was significantly correlated with TP (Fig. 1). In this study, cell volume is probably the best index of periphyton biomass because acetone extraction of chlorophyll from green algae often is incomplete (Marker 1972) and leads to serious underestimations whereas estimates of organic material could be biased by detritus and nonalgal organisms. In any case, the slopes and coefficients of determination of the regressions between all three indices of periphyton biomass and TP were much lower than those calculated for similar relations in phytoplankton (e.g. for chlorophyll (Dillon and Rigler 1974), $b = 1.45$; $r^2 = 0.90$, and for cell volume (Watson and Kalff 1981), $b = 1.43$; $r^2 = 0.88$). These much poorer relationships cannot be attributed to the peculiarity of the sampling sites, since the regression between TP and Chl *a* in phytoplankton samples collected near the periphyton (Fig. 2) was very similar in both slope ($b = 1.28$) and coefficient of determination ($r^2 = 0.89$) to those calculated for open-water phytoplankton in these lakes (Pace 1984, $b = 1.09$; $r^2 = 0.93$) and others (e.g. Dillon and Rigler 1974).

Several factors could be responsible for the scatter and shallow slope of the periphyton biomass – P relation. Some of the lakes had a low TN:TP ratio (<12), suggesting that N could be an important parameter (Smith 1982). Since N concentrations in the littoral were not available, I used values collected in open water during the same season (E. Bentzen, Departmnent of Biology, University of Waterloo, Waterloo, Ont., pers. comm.). This seems legitimate because measurements of TP in the littoral and in the open water were highly correlated ($r^2 = 0.93$). However, neither introduction of N in a multivariate analysis with P nor regression of any of the periphyton biomass indices on N alone improved the coefficients of determination.

Light, which is reduced by phytoplankton in eutrophic lakes, could contribute to the low slope of the periphyton–P relationship. However the regression between TP and periphyton chlorophyll at 1 m is very similar to the relation calculated for chlorophyll at 0.1 m of depth (Fig. 1), where the effect of reduced light can be ruled out. Moreover, when reflectance, an indirect estimate of light availability that correlates closely with Secchi disk ($r^2 = 0.80$; $n = 21$ for open-water samples), was introduced with TP in a multivariate analysis, it did not improve the prediction of periphyton biomass.

Exposure to waves could influence periphyton biomass, especially at the shallow depths I sampled (Fox et al. 1969; Young 1945). Wave intensity is related to lake morphology and wind direction. Maximum effective fetch (i.e. fetch measured along the axis that gives the highest value, Håkanson

1981) was calculated for all the sites (Table 1). When this factor was introduced in the periphyton biomass – P relationships the predictions were not improved with the exception of a slight, but significant, increase in describing periphyton chlorophyll on stones at 0.1 m ($r^2 = 0.40$). There was a positive effect of fetch on periphyton biomass at the beginning of the season that was significant enough to warrant further study (A. Cattaneo, in prep.).

The low and variable response of periphyton biomass to increased nutrients could simply be due to the fact that this community grows attached to a substrate. Rapid growth in eutrophic lakes results in very thick and unstable periphyton mats because algae in the lower strata die (Kevern et al. 1966; Neal et al. 1967). This sets an upper limit to the amount of biomass that can develop on a submerged object. This substrate saturation could uncouple biomass from production in periphyton and ultimately induce the poor relation between biomass and nutrients (Moss 1980). Indeed, the response of periphyton to fertilization is often weak (Nelson et al. 1973; Stockner and Armstrong 1971), especially in comparison with phytoplankton response in the same systems (Bjork-Bamberg 1984). Some oligotrophic lakes of British Columbia are an exception to this pattern; thus, periphyton responds sharply to fertilization (Shortreed et al. 1984). In this case, the final biomass was still too low to saturate the substrate.

Taxonomic Composition

Since total biomass of periphyton is not well correlated with TP, I examined whether some components of the community had a better relationship with nutrients. Total biomass was partitioned by taxa, life form, and size (Table 2) and the biomass of these parts correlated with TP (Table 3). In the open water, eutrophication is usually associated with blooms of blue-green algae. Smith (1983) described an inverse relationship between the proportion of blue greens in the community and N:P ratio in the water (this latter parameter tends to decrease with P enrichment). In the present study, blue-greens did not increase significantly with TP; indeed, the percentage of blue-green colonial forms (mainly *Microcystis* and *Coelosphaerium*) increased slightly, but significantly, with N:P ($r^2 = 0.36$; $P < 0.05$). The importance of periphytic blue-greens in oligotrophic lakes has been observed elsewhere (Kann 1959; Loeb and Reuter 1981) and is sometimes linked to their ability to fix N (Reuter et al. 1983). The different responses of phytoplanktonic and periphytic cyanophytes to eutrophication suggest that the N:P ratio near the sediments could differ from that of open water.

Diatoms, dominant in most periphyton assemblages (Stockner and Armstrong 1971; Ennis 1975), did not increase significantly with TP and tended to be replaced by green algae in rich sites (Table 2). Such an inverse distribution of diatoms and green algae has also been observed in Lake Huron, where the diatom component of the *Cladophora*–epiphyte complex increased with the distance from a point source of sewage discharge (Stevenson and Stoermer 1982).

In the present study, the biomass of green algae was positively correlated with TP. The taxa responding to eutrophication were mainly *Cladophora* and to a lesser degree *Ulothrix*, *Spirogyra*, and *Oedogonium*. All these algae are filamentous and so it is not surprising that when periphyton is divided according to life forms, filamentous algae are the only group significantly correlated with P (Table 3). However, diatom and blue-green filaments also contributed to this effect

TABLE 2. Biomass ($\mu m^3 \cdot 10^6 \cdot cm^{-2}$) of various size and taxonomic groups of algae at the 13 sites sampled. Data represent the averages over three samplings (late May, mid-July, late August). Values in parentheses represent the biomass of the filamentous forms in each group. Values less than $1\ \mu m^3 \cdot 10^6 \cdot cm^{-2}$ are not reported. The dominant taxa of each group were as follows. Diatoms: $<10^2\ \mu m^3$ *Achnanthes minutissima*; 10^2–$10^3\ \mu m^3$ *Cymbella ventricosa*, *Navicula* spp.; 10^3–$10^4\ \mu m^3$ *Cymbella* sp., *Navicula radiosa*; 10^4–$10^5\ \mu m^3$ *Stephanodiscus astrea*, *Rhopalodia* sp. Greens: 10–$10^3\ \mu m^3$ *Scenedesmus* spp.; 10^3–$10^4\ \mu m^3$ *Pediastrum* sp.; 10^4–$10^5\ \mu m^3$ *Oedogonium* spp., *Ulothrix* spp.; $>10^5\ \mu m^3$ *Cladophora* sp., *Spirogyra* sp. Blue-greens: $<10^2\ \mu m^3$ *Chroococcus* sp.; 10^2–$10^3\ \mu m^3$ *Phormidium* sp.; 10^3–$10^4\ \mu m^3$ *Oscillatoria* spp., *Microcystis* sp.; $>10^4$ *Lyngbya* spp. Others: *Dinobryon* sp., *Ceratium* sp.

Site	Diatoms				Greens				Blue-greens				
	$<10^2$ μm^3	10^2–10^3 μm^3	10^3–10^4 μm^3	10^4–10^5 μm^3	10^2–10^3 μm^3	10^3–10^4 μm^3	10^4–10^5 μm^3	$>10^5$ μm^3	$<10^2$ μm^3	10^2–10^3 μm^3	10^3–10^4 μm^3	10^4–10^5 μm^3	$>10^5$ μm^3	Others
Argent	14	18	53(20)	4	7	2(1)	6	2(2)	2	7(5)	9(8)	1	—	—
Brome	23	31	42(8)	12	4	3	21(21)	3(2)	—	4(3)	1(1)	—	—	9
Brompton	13	17	16(3)	—	6	2(1)	3(2)	26(26)	—	3(2)	7(7)	—	—	—
Bowker	6	11	13(7)	3(3)	2	3	4(2)	—	2	5(3)	28(20)	10(3)	—	4(3)
Lovering	20	43	69(20)	59(13)	2	16(8)	9(6)	9(9)	1	17(5)	24(19)	—	—	5(1)
Magog	10	38	192(148)	506(13)	12	13(2)	27(24)	16(16)	2	3	49(47)	219(213)	—	1
Massawippi	7	33	31(8)	4(2)	3	1	—	1(1)	1	2(1)	3(3)	—	—	1
Memphremagog–Border	42	130	84(11)	56(13)	3	3(1)	19(19)	1(1)	1	15(14)	10(8)	—	10(10)	1
Memphremagog–MacPherson	45	136	125(20)	45(3)	7	22(8)	—	—	1	11(7)	21(7)	4(4)	22(22)	—
Memphremagog–Newport	21	62	104(27)	13(2)	9	4(4)	9(9)	222(222)	1	2(2)	13(13)	4(4)	—	—
Memphremagog–Pender	11	54	66(13)	15	3	1(1)	1(1)	77(77)	—	2(1)	5(5)	2(2)	15(15)	—
Orford	73	60	22(3)	10(3)	4	8(6)	11(8)	4(4)	12(6)	19(7)	25(12)	2(2)	1	3
Waterloo	9	17	38(35)	102(12)	3	6(2)	23(18)	877(877)	—	16(3)	31(24)	48(47)	14	9

NOTE: A more detailed species list is available, at a nominal cost, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ont. K1A 0S2.

TABLE 3. Summary of the regressions between TP ($\mu g \cdot L^{-1}$) and the biomass ($\mu m^3 \cdot 10^6 \cdot cm^{-2}$) of various periphyton groups, divided according to taxonomy, life form, and size. Calculations are based on the log of the seasonal averages. In all regressions, $n = 13$. $^{**}P < 0.01$; $^{***}P < 0.001$; NS = not significant.

Equation	r^2	F	P
Diatoms = $39.4\,TP^{0.48}$	0.20	2.8	NS
Greens = $1.6\,TP^{1.21}$	0.56	13.8	**
Blue-greens = $7.6\,TP^{0.52}$	0.14	1.8	NS
Singles = $43.2\,TP^{0.42}$	0.15	2.0	NS
Colonials = $11.2\,TP^{0.47}$	0.00	0	NS
Filamentous = $3.7\,TP^{1.17}$	0.67	22.1	***
$<100\ \mu m^3$ = $38.1\,TP^{0.24}$	0.07	0.8	NS
$100-1000\ \mu m^3$ = $56.6\,TP^{-0.02}$	0.01	0	NS
$1000-10\,000\ \mu m^3$ = $29.1\,TP^{0.35}$	0.19	2.6	NS
$>10\,000\ \mu m^3$ = $1.3\,TP^{1.49}$	0.62	18.1	***

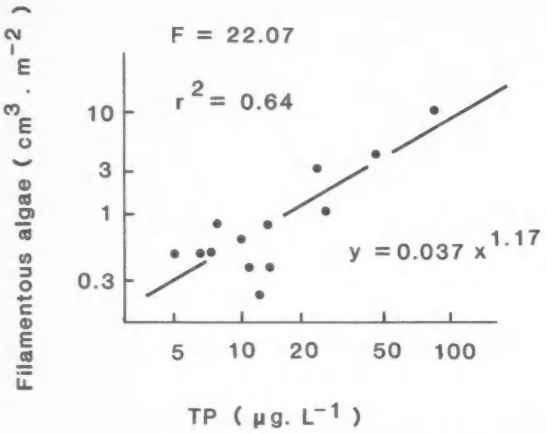

FIG. 3. Regression between TP in the water and biomass of filamentous algae on stones at 1 m of depth. Data represent seasonal averages.

TABLE 4. Summary of the log–log regressions between TP ($\mu g \cdot L^{-1}$) in the water and various estimates of periphyton biomass ($\mu m^3 \cdot 10^6 \cdot cm^{-2}$, except Chl *a* which is $mg \cdot m^{-2}$) with all the data included. $^{*}P < 0.05$; $^{***}P < 0.001$.

Equation	n	r^2	F	P
Chl *a* = $16.7\,TP^{0.20}$	88	0.05	4.3	*
Total volume = $49.5\,TP^{0.56}$	39	0.21	9.6	***
Greens = $2.4\,TP^{0.97}$	39	0.33	18.6	***
Filamentous = $6.7\,TP^{0.87}$	39	0.31	16.8	***
$>10\,000\ \mu m^3$ = $1.6\,TP^{1.28}$	39	0.36	20.6	***

so that the relationship between TP and all filamentous is slightly better than by considering only green filaments ($r^2 = 0.51$). The dominance of filamentous forms in eutrophic sites reflects the enhanced light penetration and nutrient transport provided by their morphology when the available substrate is saturated. These algae thrive at high P concentration and often impair the recreational value of the lake, for they clog water intakes and foul the shore when they decay. Excessive growth of green filaments, especially *Cladophora*, has long been associated with eutrophication (Evans and Stockner 1972; Ennis 1975), and their distribution, seasonality, and nutrient kinetics have been extensively studied in the Great Lakes (Auer and Canale 1982). The relationship between biomass of filamentous algae and TP observed in the present study (Fig. 3) has still too much scatter to provide a fine management tool but is the only quantification in a series of lakes of this widely reported tendency.

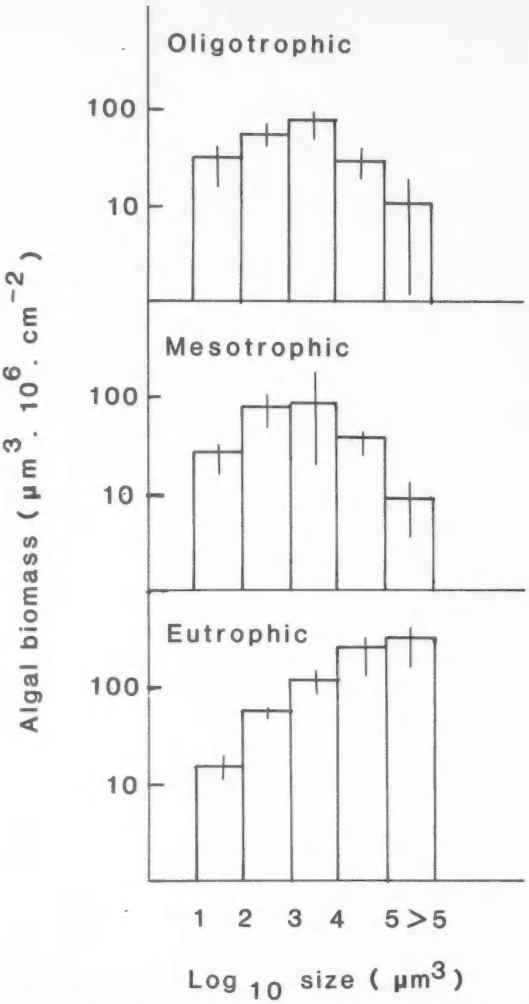

FIG. 4. Size distribution of algal biomass in oligotrophic (TP < 8 $\mu g \cdot L^{-1}$), mesotrophic (TP = 8–20 $\mu g \cdot L^{-1}$), and eutrophic (TP > 20 $\mu g : L^{-1}$) sites. Data represent averages over the season and over the sites, and bars represent their standard errors; $n = 12$ except in the middle panel where $n = 15$.

Size Distribution

When the algal community was divided into logarithmically increasing size classes (Sheldon et al. 1972), only the biomass of algae greater than 10000 μm^3 was significantly correlated

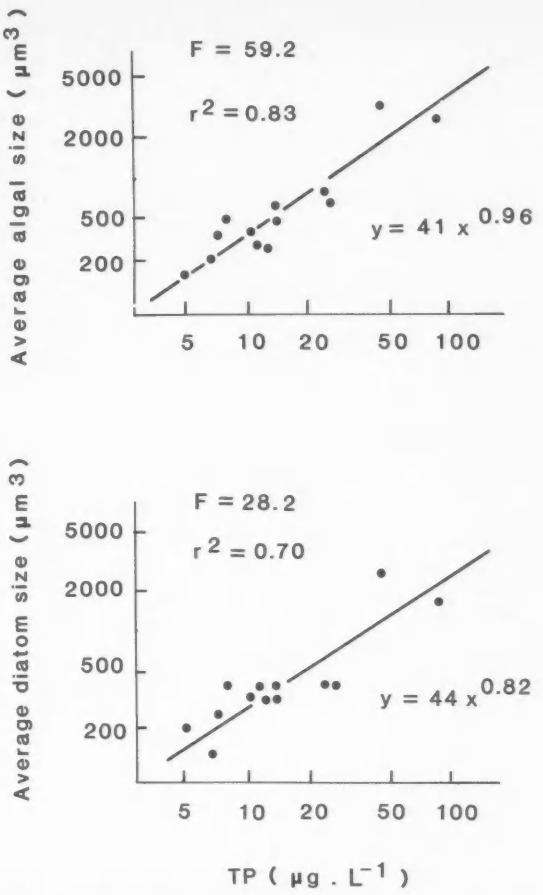

FIG. 5. Regressions between TP in the water and the average algal size (top panel) and the average diatom size (bottom panel). Data represent seasonal averages. $P < 0.001$ for both regressions.

with TP (Table 3). This is reflected in the biomass size distribution at the various sites (Fig. 4). For a simplified presentation, the data have been grouped in three categories (Vollenweider 1968): oligotrophic (TP < 8 µg·L^{-1}), mesotrophic (TP $= 8-20$ µg·L^{-1}), and eutrophic (TP > 20 µg·L^{-1}). Biomass of the smaller algae (<10000 µm^3), readily available to grazers, is rather similar at all sites, while large size classes are much more prominent in eutrophic lakes. These large, mostly filamentous algae are scarcely utilized (Canale and Auer 1982) and even then mainly by large grazers (Tricoptera and Coleoptera, Gaevskaya 1966). These size distributions suggest that algae less than 10000 µm^3 in size are kept at similar levels at all sites either by proportionally higher grazing or self-shading in eutrophic sites. On the other hand, large algae, protected by their size against grazers, are better able to grow at high nutrient levels (Shuter 1978). Since large, filamentous algae grow better at eutrophic sites, it is not too surprising that average algal size is well correlated with TP (Fig. 5). It is more surprising that this relationship is significant even when only diatoms are considered (Fig. 5). These findings in the periphyton agree with the observation in phytoplankton that the proportion of large algae increases with trophy (Watson and Kalff 1981) and with the general theory that increased resource supply leads to communities with larger individual size (Peters 1983)

Seasonality

When, instead of seasonal averages, individual measurements of the various periphyton parameters and TP are correlated (Table 4), the trends are similar to those discussed earlier (cf. Table 3). Consequently, periphyton seasonal changes are not simply the result of seasonal changes in TP.

Seasonal changes in biomass are often large and follow different patterns in different lakes. High spring values followed by a summer low were observed in most of the oligotrophic and mesotrophic lakes, but this pattern was stronger in the latter (Fig. 6). Summer maxima were instead observed in three of the four eutrophic sites (Fig. 6). Seasonal trends were similar at 0.1 and 1 m, even if values at 0.1 m tended to be lower than at 1 m, probably reflecting heavier wave action at shallow depth (Fox et al. 1969). Sharp summer declines following spring maxima have been repeatedly observed in periphytic and planktonic communities of unenriched waters (Round 1981) and linked to grazing (Lampert and Schober 1978; Cattaneo 1983). Peaks of biomass also occur in summer in eutrophic lakes (Davis 1964). In this study, they follow the preference for most green filamentous algae for temperature around 20°C (Blum 1982).

Since taxonomic composition and size distribution were estimated only three times during the study, seasonal changes of these variables are less clear. Considering all sites, there was a significant tendency for the diatom fraction to decrease during the summer, while the importance of the other taxonomic groups, life forms, and average algal size did not show a significant seasonal change (Wilcoxon signed rank test).

Conclusions

This study has shown that periphyton respond to eutrophication differently than phytoplankton. The response of periphyton total biomass is less pronounced and more variable. Fringing mats of filamentous green algae, rather than blue-green blooms, characterize the richest sites. While nannoplankton is significantly correlated with TP (Watson and Kalff 1981), in periphyton only large forms are. However, in both communities the importance of large algae increase with trophy.

In periphyton, P reduction would preferentially affect the large filamentous algae that foul lake shores during the period of maximum recreational use and largely leave unchanged the biomass of diatoms and others smaller algae, to serve as a source of food for the littoral zone.

Although there were significant trends in the relationships between periphyton taxonomy or size distribution and TP, much variation remains unexplained. Consideration of N and light availability, which had proven to affect the phytoplankton, failed to improve the periphyton predictions. Other variables which are more specific to the periphyton community, such as fetch, slope, substrate quality, and size, may well be important determinants of periphyton biomass and deserve further study.

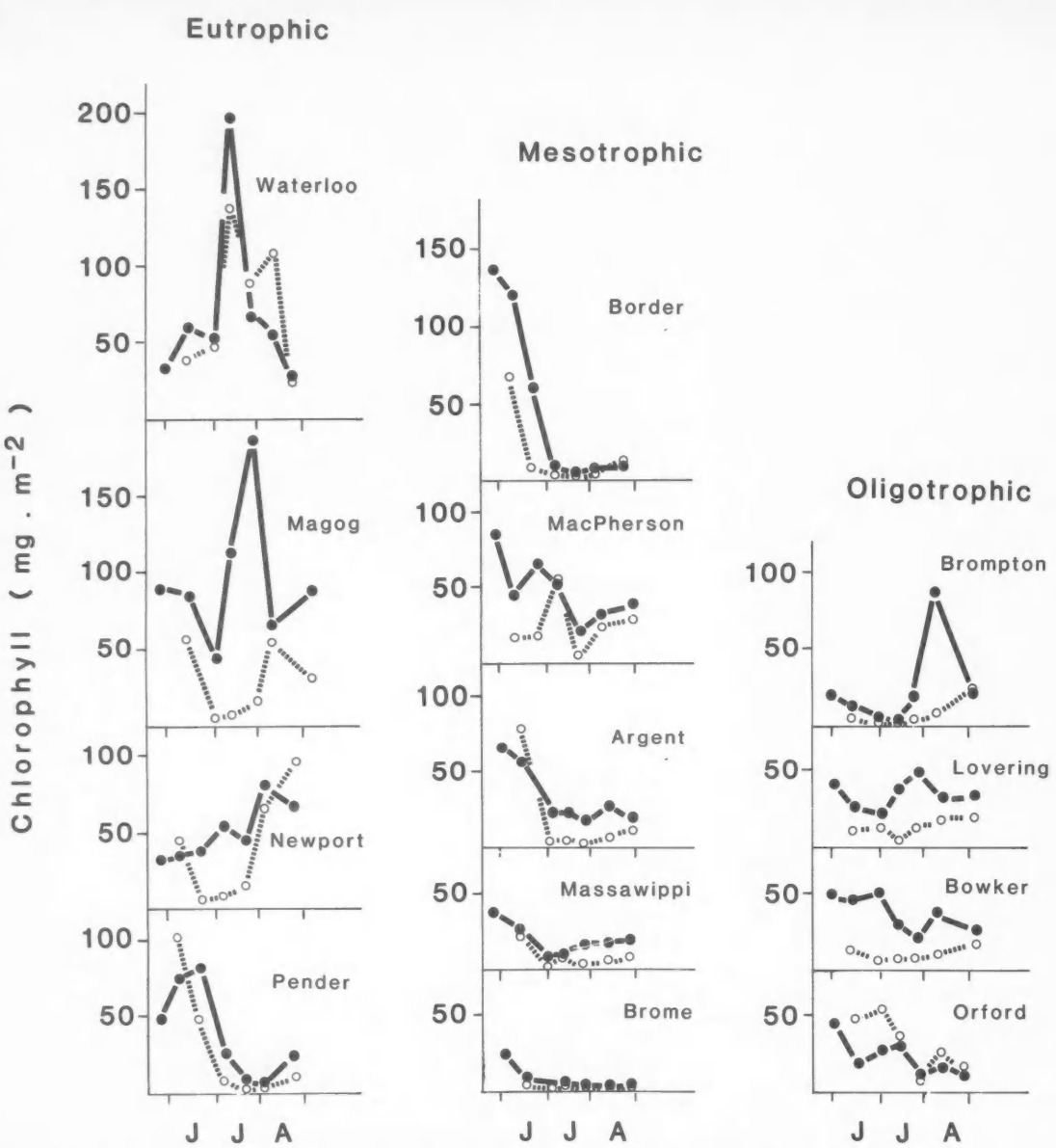

FIG. 6. Seasonal changes of periphyton biomass (as Chl *a*) on stones at 0.1 (broken line) and 1 m (solid line) at the various sites.

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References

AUER, M. T., AND R. P. CANALE. 1982. Ecological studies and mathematical modelling of *Cladophora* in Lake Huron: 2. Phosphorus uptake kinetics. J. Great Lakes Res. 8: 84–92.

AUER, M. T., R. P. CANALE, H. C. GRUNDLER, AND Y. MATSVOKA 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 1. Programm description and field monitoring of growth dynamics. J. Great Lakes Res. 8: 73–83.

BERGMANN, M., AND R. H. PETERS. 1980. A simple reflectance method for the measurements of particulate pigment in lake water and its application to phosphorus–chlorophyll–seston relationships. Can. J. Fish. Aquat. Sci. 37: 111–114.

BIRD, D., AND J. KALFF. 1984. The empirical relationship between bacterial abundance and chlorophyll concentration in aquatic systems. Can. J. Fish. Aquat. Sci. 41: 1015–1023.

BJORK-BAMBERG, S. 1984. Species composition and biomass of an epipelic algal community in a subartic lake before and during fertilization.

Holarct. Ecol. 7: 195–201.

BLUM, J. L. 1982. Colonization and growth of attached algae at the lake Michigan water line. J. Great Lakes Res. 8: 10–15.

CANALE, R. P., AND M. T. AUER. 1982. Ecological studies and mathematical modeling of *Cladophora* in Lake Huron: 5. Model development and calibration. J. Great Lakes Res. 8: 112–125.

CATTANEO, A. 1983. Grazing on epiphytes. Limnol. Oceanogr. 28: 124–132.

CATTANEO, A., AND J. KALFF. 1980. The relative contribution of aquatic macrophytes and their epiphytes to the production of macrophytes beds. Limnol. Oceanogr. 25: 280–289.

CHAMBERS, P. A., AND J. KALFF. 1985. Depth distribution and biomass of submerged aquatic macrophytes communities in relation to Secchi depth. Can. J. Fish. Aquat. Sci. 42: 701–709.

DAVIS, C. C. 1964. Evidence for the eutrophication of Lake Erie from phytoplankton records. Limnol. Oceanogr. 9: 275–283.

DILLON, P. J., AND F. H. RIGLER. 1974. The phosphorus–chlorophyll relationship in lakes. Limnol. Oceanogr. 19: 767–773.

ENNIS, G. L. 1975. Distribution and abundance of benthic algae along phosphate gradients in Kootenay Lake, British Columbia. Verh. Int. Ver. Limnol. 19: 562–570.

EVANS, D., AND J. G. STOCKNER. 1972. Attached algae on artificial and natural substrates in Lake Winnipeg, Manitoba. J. Fish. Res. Board Can. 29: 31–44.

FOX, J. L., T. O. OLAUG, AND T. A. OLSON. 1969. The ecology of periphyton in Western Lake Superior. I. Taxonomy and distribution. Bull. Water Resour. Res. Cent. Univ. Minn. 14: 1–97.

GAEVSKAYA, N. S. 1966. The role of higher aquatic plants in the nutrition of the animals of fresh-water basins. Academy of Science of the U.S.S.R. 629 p. (Transl. from Russian by Lending Library for Science and Technology, England)

HÅKANSON, L 1981. A manual of lake morphometry. Springer-Verlag, New York, NY. 78 p.

HORNER, R. R., AND E. B. WELCH. 1981. Stream periphyton development in relation to current velocity and nutrients. Can. J. Fish. Aquat. Sci. 38: 449–457.

KANN, E. 1959. Die eulittorale Algenzone in Tramsee (Oberosterreich). Arch. Hydrobiol. 55: 129–192.

KEVERN, H. R., J. L. WILHM, AND G. M. VAN DYNE. 1966. The use of artificial substrata to estimate the productivity of periphyton. Limnol. Oceanogr. 11: 499–502.

KREWER, J. A., AND H. W. HOLM. 1982. The phosphorus – chlorophyll *a* relationship in periphytic communities in a controlled ecosystem. Hydrobiologia 94: 173–176.

LAMPERT, W., AND U. SCHOBER. 1978. Das regelmassige auftreten von fruhjahrsalgenmaximum und "klarwasserstadium" im Bodensee als folge von klimatischen bedingungen und wechselwirkungen zwischen phyto- und zooplankton. Arch. Hydrobiol. 82: 364–386.

LOEB, S. L. 1981. An in situ method for measuring the primary productivity and standing crop of the epilithic periphyton community in lentic systems. Limnol. Oceanogr. 26: 394–399.

LOEB, S. L., AND J. E. REUTER. 1981. The epilithic periphyton community: a five-lake comparative study of community productivity, nitrogen metabolism, and depth distribution of standing crop. Verh. Int. Ver. Limnol. 21: 346–352.

MARKER, A. F. H. 1972. The use of acetone and methanol in the estimation of chlorophyll in the presence of phaeophytin. Freshwater Biol. 2: 361–385.

MENZEL, D. W., AND H. CORWIN. 1965. The measurement of total phosphorus based on the liberation of organically bound fractions by persulfate oxidation. Limnol. Oceanogr. 10: 280–282.

MOSS, B. 1980. Periphyton biomass, p. 151–152. *In* E. D. LeCren, and R. H. Lowe-McConnel [ed.] The functioning of freshwater ecosystems. Cambridge University Press, London.

NEAL, E. C., B. C. PATTEN, AND C. E. DEPOE. 1967. Periphyton growth on artificial substrates in a radioactively contamined lake. Ecology 48: 918–924.

NELSON, R. R., T. O. ODLAUG, B. O. KROGSTAD, O. R. RUSCHMEYER, AND T. A. OLSON. 1973. The effects of enrichment on Lake Superior periphyton. Bull. Water Resour. Res. Cent. Univ. Minn. 59: 1–182.

NICHOLLS, K. H., AND P. J. DILLON. 1978. An evaluation of phosphorus–chlorophyll–phytoplankton relationships for lakes. Int. Rev. Gesamten Hydrobiol. 63: 141–154.

PACE, M. L. 1984. Zooplankton community structure, but not biomass, influences the phosphorus – chlorophyll *a* relationship. Can. J. Fish. Aquat. Sci. 41: 1089–1096.

1986. An empirical analysis of zooplankton community size structure across lakes trophic gradients. Limnol. Oceanogr. 31: 45–55.

PETERS, R. H. 1983. The ecological implications of body size. Cambridge University Press, London. 329 p.

PETERS, R. H., AND M. BERGMANN. 1986. The relationship between transparency and reflectance. Mem. Ist. Ital. Idrobiol. 43: 77–89.

REUTER, J. E., S. L. LOEB, AND C. R. GOLDMAN. 1983. Nitrogen fixation in periphyton of oligotrophic Lake Tahoe, p. 101–109. *In* R. G. Wetzel [ed.] Periphyton of freshwater ecosystems. Developments in hydrobiology 17. Dr. W. Junk Publishers, The Hague.

ROUND, F. E. 1981. The ecology of algae. Cambridge University Press, London. 653 p.

SHELDON, R. W., A. PRAKASH, AND W. H. SUTCLIFFE. 1972. The size distribution of particles in ocean. Limnol. Oceanogr. 17: 327–340.

SHORTREED, K. S., A. C. COSTELLA, AND J. G. STOCKNER. 1984. Periphyton biomass and species composition in 21 British Columbia lakes: seasonal abundance and response to whole-lake nutrient addition. Can. J. Bot. 62: 1022–1031.

SHUTER, B. J. 1978. Size dependence of phosphorus and nitrogen subsistence quotas in unicellular organisms. Limnol. Oceanogr. 23: 1248–1255.

SMITH, V. H. 1982. Predicting the effects of eutrophication responses in the phytoplankton, p. 249–264. *in* E. M. O. Loughlin and P. Cullen [ed.] Prediction in water quality. Australia Academy of Science, Camberra.

1983. Low nitrogen: phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. Science (Wash., DC) 221: 669–671.

SOSZKA, G. J. 1975. The invertebrates on submerged macrophytes in three Masurian lakes. Ekol. Pol. 23: 371–391.

SPRULES, G. W., AND R. KNOECHEL. 1985. Lake ecosystem dynamics based on functional representations of trophic components, p. 383–403. *In* D. G. Meyers and J. R. Strickler [ed.] Trophic interactions within aquatic ecosystems. A.A.A.S. Selected Symposium. Westview Press, Boulder, CO. 427 p.

STEVENSON, R. J., AND E. F. STOERMER. 1982. Abundance patterns of diatoms on *Cladophora* in Lake Huron with respect to point source of wastewater treatment plant effluent. J. Great Lakes Res. 8: 184–195.

STOCKNER, J. G., AND F. A. J. ARMSTRONG. 1971. Periphyton of the Experimental Lakes Area (ELA), northwestern Ontario. J. Fish. Res. Board Can. 28: 215–229.

STRICKLAND, J. D. H., AND T. R. PARSONS. 1972. A practical handbook of seawater analysis. 2nd ed. Bull. Fish. Res. Board. Can. 167: 310 p.

VOLLENWEIDER, R. A. 1968. Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. Tech. Rep. OECD Paris, DAS/CSI/68, 27: 159 p.

WATSON, S., AND J. KALFF. 1981. Relationships between nannoplankton and lake trophic status. Can. J. Fish. Aquat. Sci. 38: 960–967.

YOUNG, O. W. 1945. A limnological investigation of periphyton in Douglas Lake, Michigan. Trans. Am. Microsc. Soc. 64: 1–20.

Relation between Aiming and Catch Success in Larval Fishes

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The actual attack of prey by common carp (*Cyprinus carpio*) and northern pike (*Esox lucius*) larvae, lasting 5–20 ms, was described using high-speed cinematography showing synchronous lateral and ventral views. The accuracy of aiming at the prey was measured. A model comparing the ratio mouth radius/aiming inaccuracy to catch success of stationary prey accurately predicted catch success for larval carp feeding on *Artemia* nauplii and for larval pike feeding on *Daphnia*. The increase in catch success during ontogeny was caused by an increase in the ratio mouth radius/aiming inaccuracy. Maximal suction velocity in the water flow created by pike larvae (14 mm standard length) was 0.84 m/s, much higher than the escape velocities of even calanoid copepods. Nevertheless, even *Daphnia* could sometimes escape the suction flow by jumping away. The relative importance of aiming and speed of attack on catch success depended on prey species. Prey size seemed unimportant in determining catch success.

Le filmage à grande vitesse permettant de prendre des vues latérales et ventrales synchrones a servi à montrer l'attaque d'une proie par des larves de carpe commune (*Cyprinus carpio*) et de grand brochet (*Esox lucius*) qui a duré de 5 à 20 ms. On a aussi mesuré la précision de l'attaque. Un modèle comparant le rapport diamètre de la bouche/imprécision de l'attaque avec le succès de capture de proies stationnaires a prédit exactement le succès de capture obtenu par des larves de carpe se nourrissant de nauplii d'*Artemia* et des larves de brochet se nourrissant de *Daphnia*. L'augmentation du succès de capture pendant l'ontogénèse était le résultat d'une augmentation du rapport diamètre de la bouche/imprécision de l'attaque. La vitesse maximum de succion dans l'eau créée par les larves de brochet (longueur standard : 14 mm) s'élevait à 0,84 m/s, une valeur beaucoup plus élevée que les vitesses des copépodes calanoïdes en fuite. Toutefois, les *Daphnia* pouvaient parfois s'échapper du tourbillon créé par la succion en faisant un bond. L'importance de la précision et de la vitesse de l'attaque par rapport au succès d'une capture dépend de l'espèce de la proie. La taille de la proie ne semble pas importante dans la détermination du succès de capture.

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It is widely believed that predation and starvation are the dominant causes of the extensive mortality of fish larvae (e.g. Blaxter 1969), predation being probably the most important factor (Oiestad 1984).

The rate of feeding depends on the opportunities for encountering prey and capturing them. The first depends on the swimming velocity as well as the distance at which the prey is detected and reacted to (reactive distance) (Braum 1967; Hunter 1972; Confer and Blades 1975). The latter depends on the accuracy in aiming at the prey during the strike, i.e. snapping at the right place (Beyer 1980), and the speed of the strike, i.e. preventing the prey from jumping away (Drenner et al. 1978; Winfield et al. 1983; Mills et al. 1984). The actual strike is of very short duration, less than 15 ms for first feeding stages of larval common carp (*Cyprinus carpio*) (Drost and van den Boogaart 1986b). During the preparatory phase the body is curved as the larva aims at the prey, and then the larva darts forward and increases the volume of the mouth cavity to overcome the effects of stagnation while sucking the prey into the mouth cavity. A complete description is given under Results and Discussion.

Catching strategy improves rapidly during the growth of fish larvae (Table 1). Larvae that are larger at the time of hatching (more mature) are more efficient at catching prey (e.g. northern pike (*Esox lucius*)); small larvae of some species have a high initial catch success (e.g. bigeye (*Anchoa lamprotaenia*) and bay anchovy (*A. mitchilli*)). Also, larvae often have different rates of success for different prey, even when prey are of equal size (see Table 1).

In order to relate the extensive change in form of fish larvae during ontogeny with their increase in catch success, it is important to know whether this increase is due mainly to an improvement in speed or aiming.

In this paper, I describe food intake in larval carp and pike and investigate the causes of the rapid increase in catch success during ontogeny and the significance of aiming of the predator and escape movements of the prey on the catch success of fish larvae.

Materials and Methods

Definitions

A strike is defined as a lunge forward while increasing the volume of the mouth cavity rapidly. Catch success is the

TABLE 1. Catch success of fish larvae. Success is percentage successful of all snaps. Age is given relative to hatching; ff = first-feeding, SL = standard length; Prey: A = nauplii of *Artemia salina*, B = *Brachionus*, D = *Daphnia* of equal size to *Artemia* nauplii, MZ = mixed zooplankton, MZS = mixed zooplankton passing through a 110-μm-sieve and retained by a 53-μm-mesh sieve.

Species	Common name	Success	Age	SL (mm)	Prey	Reference[b]
Engraulis mordax	Northern anchovy	10	ff (3 d)	3.8	B	1
		81	17 d	8.3	B	1
		37	17 d	8.3	A	1
Clupea harengus	Herring	7[a]	ff	??	A	2
		95[a]	7 wk	??	A	2
Esox lucius	Northern pike	30	0–3 d since ff	??	MZ	3
		80.5	15 d since ff	??	MZ	3
Coregonus fera	Weissfelchen	4.8	0–8 d since ff	??	MZ	3
		18.3	9–16 d since ff	??	MZ	3
C. wartmanni	Blaufelchen	3.2	0–8 d since ff	??	MZ	3
		21.6	9–16 d since ff	??	MZ	3
Anchoa mitchilli	bay anchovy	36.5	ff (2 d)	2.7	MZS	4
		51.6	8 d	3.9	MZS	4
A. lamprotaenia	bigeye anchovy	50.3	ff (2 d)	3.6	MZS	4
		70.0	8 d	5.5	MZS	4
Alosa sapidissima	American shad	43	6 d	10.3	A	5
		50	12 d	10.5	A	5
Cichlasoma managense		70	ff	9.2	A	6
		6–7	ff	9.2	D	6
Cyprinus carpio	Common carp	51.2	ff (2 d)	5.7	A	7
		88.5	5 d	7.4	A	7

[a]These values are calculated from their fig. 5 as successful of total finished as opposed to the more quoted values of successful of total (finished + unfinished) snaps.

[b]References: 1, Hunter (1972); 2, Blaxter and Staines (1971); 3, Braum (1963); 4, Chitty (1981); 5, Wiggins et al. (1985); 6, Meyer (1986); 7, this study.

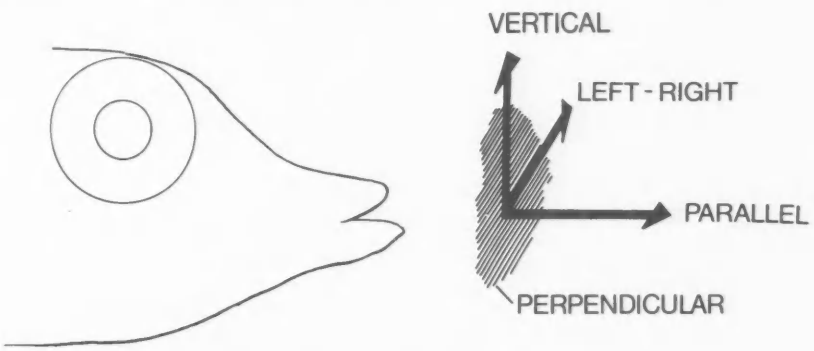

FIG. 1. Definition of the directions used.

percentage of successful snaps over their total number; this is also called feeding success (e.g. Hunter 1980), capture success (Mills et al. 1984), or capture efficiency (Meyer 1986).

Aiming can be characterized by three perpendicular directions: left–right, vertical, and parallel to the length axis of the larva (Fig. 1). Here, I consider left–right and vertical aiming together as being perpendicular aiming and aiming parallel to the length axis as parallel aiming. Inaccuracy of aiming can be quantified as distances or as angles. Distances and perpendicular aiming are considered here. The reason for leaving out parallel aiming is treated under Results and Discussion. The method for determining the accuracy of aiming of a snap is summarized in Fig. 2a. The position of the centroid of the projection of the prey was determined at the film-frame before the mouth starts to open. The length axis, which related to the mouth cavity (unless otherwise indicated), was a line in the main direction of the mouth cavity passing through the middle of the mouth aperture. For successful snaps the position of the length axis was determined at the frame the prey entered the mouth; for unsuccessful snaps it was determined at the film-frame of maximal mouth aperture because this moment coincides with prey uptake in adult fishes (Muller and Osse 1984). The distance between the centroid of the prey and this length axis is called the projected perpendicular uptake distance (ppud). It could be positive (prey located to the left of or above the length axis) or negative. For each snap a vertical and a left–right ppud could be measured. The perpendicular uptake distance (pud), the pythagorean sum of vertical and left–right

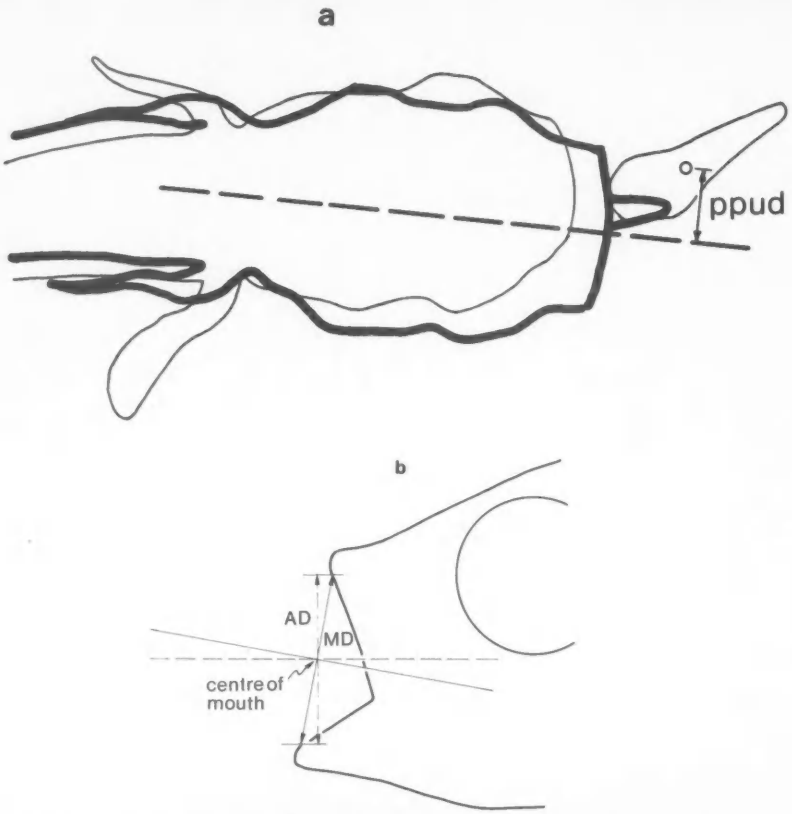

FIG. 2. (a) Accuracy of aiming was determined from the film as shown in this example of the ventral view of a carp larva (5.8 mm). The position of the larva and the prey are drawn at two times: at the film-frame just prior to the start of mouth opening (light lines) and at the film-frame at which the centre of mass of the prey passes through the mouth aperture (bold lines). The broken line is the length axis of the mouth cavity. The projected perpendicular uptake distance (ppud) is the distance between the centroid of the prey at the film-frame just before the start of mouth opening (circle) and the length axis at the film-frame of prey uptake. (b) If the mouth aperture was not perpendicular to the length axis (horizontal broken line), two errors occurred. First the mouth radius was overestimated; compare the measured distance (MD) with the real distance (AD), a difference of 2.5% in this situation. The ppud should be measured relative to the length axis of the mouth cavity but was measured relative to the horizontal solid line. The latter error increased with increasing measured distance parallel to length axis of the fish between prey and centre of mouth.

ppud, was the measure of accuracy of aiming at one particular snap. The aiming inaccuracy, i.e. the standard deviation of ppuds, represented the measure for several snaps.

If the prey did not actively move, it still moved because of the suction effect towards the length axis of the mouth cavity (Muller and Osse 1984; Muller and van Leeuwen 1985). A later determination of the position of the prey would have underestimated the ppud; conversely, if the prey actively moved, the ppud would have been overestimated.

I assumed that the fish aimed just prior to the onset of suction and that it did not adjust its movements later, even if the prey made escape movements. Large changes during the suction process were almost impossible due to its short duration (Osse and Muller 1980).

Prior to constructing a model for the relation between aiming and catch success, the following notions needed to be defined. The aiming target is the mean of the measured ppuds, and the aiming inaccuracy is their standard deviation. Assuming that the fish aimed at the centre of mass of the prey, the expected value of the aiming target was zero. The aiming inaccuracy was also called aiming accuracy by Beyer (1980), but the latter terminology was avoided here because a higher value for the aiming accuracy corresponded then to a less accurately aiming fish.

Accuracy of the Measurements

In small carp larvae (6–8 mm standard length (SL)), the lateral and dorso-ventral head movements during a snap were very extensive (see e.g. Fig. 4 and 5); in pike larvae the movements of the head perpendicular to the swimming direction were small compared with the movement parallel to it. For carp the measured position of the axis of the mouth cavity was

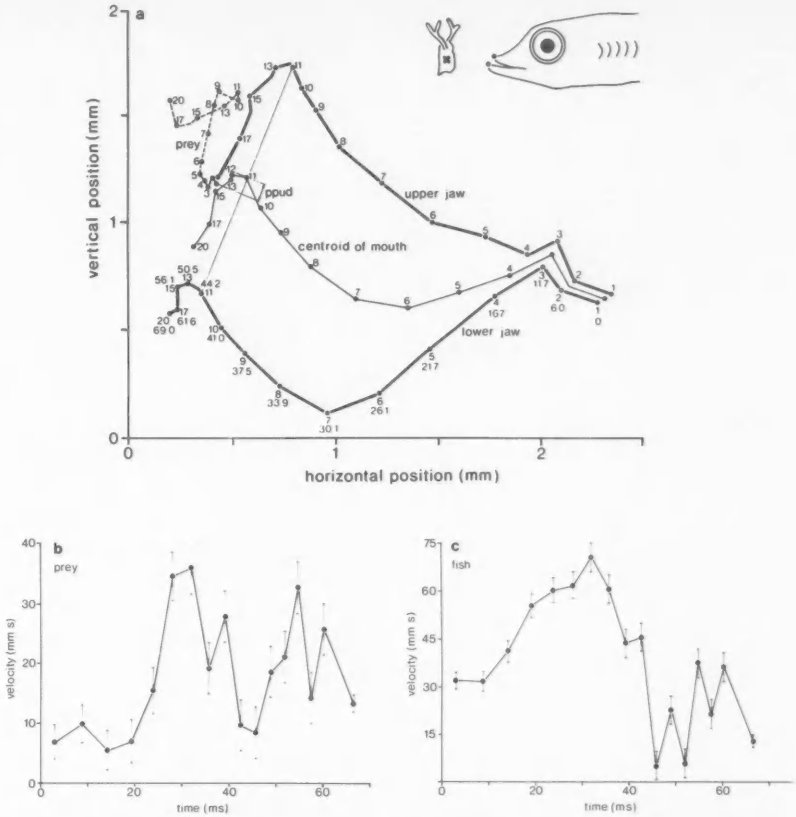

FIG. 3. Example of an unsuccessful suction act of a 14-mm pike larva feeding on a *Daphnia*. The film was accelerating from approximately 170 fr/s in frame 1 to 400 fr/s in frame 20. Errors were estimated from the inaccuracy of measurement. (a) Movements of upper and lower jaws, centroid of the mouth, and centre of mass of the prey in lateral projection. Numbers indicate successive frames. Time for each film-frame (ms) is indicated near the curve of the lower jaw, starting from the last film-frame in which the mouth is just closed (frame 1). (b) Velocity of the prey. First the prey was stationary (frames 1–4). Then it jumped away (frames 5–9); maximal acceleration = 5.2 m/s^2 (error 1.7). At frame 9 the centre of mass of the prey was just in front of the fish's upper jaw. Between frames 9 and 10 it is sucked toward the mouth aperture. In frame 11 it has collided with the upper lip and was pushed forward. At frame 20 the prey started a second jump and definitively escaped (not shown in this figure). (c) Velocity of the middle of the mouth aperture. It accelerated from 0.03 to 0.07 m/s and then decelerated. The stark oscillation in the velocity after t = 45 ms is surprising; there was no reason for an increase in inaccuracy of measurement.

thus strongly dependent on the exact time of measurement. The precision of measurements of the ppud for carp was therefore less than for pike. Pike juveniles were fed fish, which are elongate. Many prey fish were grasped between the pike's teeth, so that there was no direct need to aim at the centre of mass. Measurements assumed this anyway. Measuring the aiming distance in the ventral view posed no problems because the fish's morphology and movements are symmetrical. In the lateral view, two problems existed. The first is that the line from the tip of the upper jaw to the top of the lower jaw is not exactly perpendicular to the length axis (Fig. 2b). This assumption introduced an error in the measurements. This error increases with increasing distance, parallel to the length axis, between the mouth aperture and centre of the prey. Fortunately this distance was generally very small (less than 0.5 mouth radius). The effective mouth radius is also slightly overestimated (by less than 10%). The second problem was that the centre of the mouth aperture moved laterally because upper and lower jaws move asynchroneously. The vertical ppud was then also susceptible to the exact time of measurement. The position of the prey was considered to be the centroid of its projection in the lateral or ventral view. Strictly speaking, this was wrong because the mass distribution in the third dimension was neglected. The error seemed to be negligible for *Daphnia* and *Artemia*, but not for fish.

Filming Setup

In total, 30 snaps of larval and juvenile pike and carp were filmed with a Teledyne DBM 54 camera (200–400 fr/s) or a Hadland Hyspeed camera (500–1150 fr/s). Shadow cin-

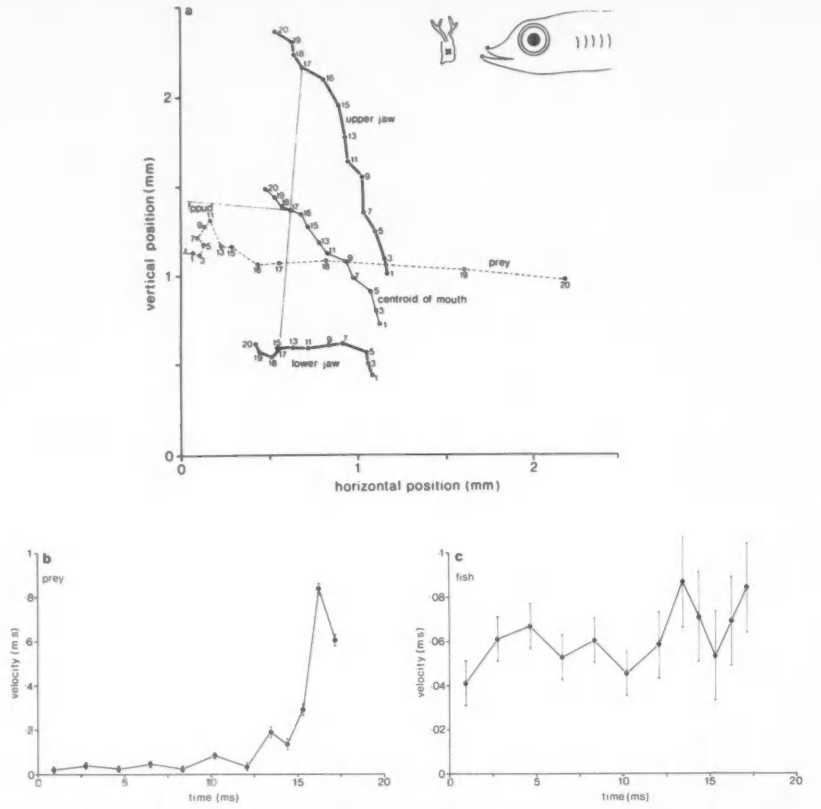

FIG. 4. Example of a successful suction act of a 14-mm pike larva feeding on a *Daphnia*. The film speed was 1077 fr/s. First, every second frame was measured, and then later every frame. Errors were estimated from the inaccuracy of measurement. (a) Movements of upper and lower jaws, centroid of the mouth, and centroid of mass of the prey in lateral projection. Numbers indicate successive film-frames. Time for each film-frame (ms) is indicated near the curve of the upper jaw. Only the opening phase of the mouth is given. Aiming was worse than in Fig. 3; the ppud was higher. (b) Earth-bound velocity of the prey. The prey made no escape movements. The measured velocity was first about 0.04 m/s. The prey was accelerated by the suction current, its maximal velocity being 0.84 m/s. (c) Velocity of the centre of the mouth aperture. Within the accuracy of the measurements the velocity of the fish was almost constant.

ematography was used (Arnold and Nuttall-Smith 1974; cf. Drost and van den Boogaart 1986b for details). Illumination strength was about 800 lx. The fishes never appeared stressed by the lights. Synchronous lateral and ventral views were obtained by three surface-coated mirrors. The films were projected with a single-frame projector (Analector 6, Oldelft) and analysed on a digitizer (Summagraphics supergrid) connected to a computer (Digital MINC 11).

Experimental Animals and Prey

Carp were from our laboratory stock kept at 23°C. Larvae were reared in 10-L aquaria equipped with an air water lift and a filter (Tetra Briljant). Carp were fed once or twice a day on nauplii of brine shrimp (*Artemia salina*). The eggs collected from pike in ponds were kindly supplied by the OVB (Dutch Organisation for Improvement of the Inland Fisheries). Pike larvae were kept at 16–18°C in 15-L aquaria. They were fed once or twice a day a mixture of zooplankton, consisting mostly of *Daphnia*. Once they reached 30 mm SL, they were fed carp larvae.

In all experiments in which distances were measured, carp larvae (6–8 mm) were fed free-swimming *Artemia* nauplii, and pike larvae (14 mm) were fed free-swimming *Daphnia* (length 0.8–1 mm, excluding spine). In the experiments with pike juveniles (62 mm), prey fish were tied to a 0.1-mm nylon thread. A greater magnification could be achieved using restrained prey. These were positioned exactly in the middle of the field of view by means of a micromanipulator. They were less active than free-swimming prey. To stimulate the feeding of the fish and to prevent habituation to restrained prey, one or two free-swimming prey were released in the filming aquarium when a restrained prey was introduced. In experiments with free-swimming prey, width and height of the aquarium were at least equal to the total length of the fish. The length of the aquarium was at least twice the length of the larva. When a prey was restrained in its movements, all dimensions were at least 1.5 times larger.

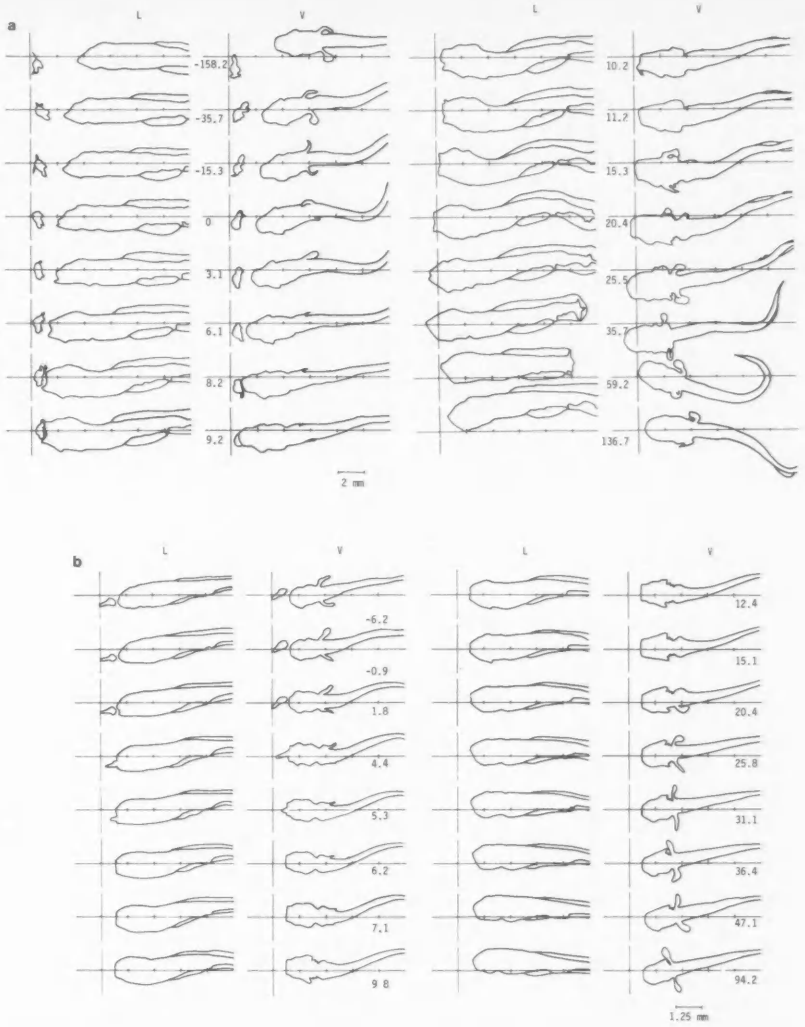

FIG. 5. Traces from high-speed movies of larvae while sucking prey. Corresponding lateral (L) and ventral (V) views are depicted next to each other. Time, relative to the last film-frame that the mouth is still closed, is indicated near the axis of the frame. Movements can be seen relative to the stationary frame. If the finfold shows its maximal size in the lateral view and is invisible in the ventral view, the fish is not rotated; otherwise, the degree of rotation can be estimated from the relative apparent size of the finfold in lateral and ventral views. The posterior region of the larvae is not always in view, and the lateral and ventral views may be slightly translated relatively to each other. In evaluating the relative distance covered by suction and swimming, it must be noted that, even if no earth-bound suction velocity occurs, suction is important in preventing stagnation (van Leeuwen 1984). In both snaps the pectoral fins became folded against the body (folded completely at the actual intake). (a) Pike, 12.5 mm SL, feeding on a restrained copepod. The bending of the body (S-posture) and movements of the pectoral fins started about 150 ms prior to the onset of suction. Apart from extensive lateral bending (maximal at 0 and 60 ms), a dorso-ventral bending occurred, maximal at 15.3 ms. A possible explanation was that contraction of the epaxial muscles caused elevation not only of the neurocranium, but also of the tail region. Therefore, contraction of the epaxial seemed stronger than of the hypaxial musculature. The prey was almost stationary in the earth-bound frame. (b) Carp, 6.5 mm SL, feeding on an *Artemia* nauplius from just above the bottom. This snap was not very intensive; compare the intensive snap of a 5.8-mm carp larva in Drost and van den Boogaart (1986b). The bending of the body and rotation of the length axis of the mouth cavity was small. In other snaps of carp larvae, the head and tail moved upwards as in the snap of the pike larva in Fig. 5a. About two thirds of the initial prey distance was covered by suction and only one third by swimming.

In order to make reliable measurements the magnification of the film negative had to be high. Using free-swimming prey, the aquaria had to be small to have at least some snaps in the field of view. With restrained prey the magnification could be high, irrespective of the size of the aquarium.

Results and Discussion

Suction Process of the Pike

Prior to the suction motion itself, a first-feeding larva (12–15 mm SL) generally slowly approached the prey, mostly by movements of the pectoral fins (see Fig. 5a). It then formed a S-shaped attack posture, the duration of which depended on the type of prey. When pike fed on very sluggish prey (e.g. nauplii of *Artemia salina*) the posture was virtually absent; but when feeding on evasive prey (calanoid copepods) it was prominent (see Fig. 5a) and sometimes lasted for several seconds. In older larvae the attack posture was no longer distinct and became integrated in the swimming movements. Suction started when the larvae straightened and almost simultaneously increased the volume of their mouth cavity by opening their mouth. In first-feeding pike larvae the prey entered the mouth within 15–20 ms after the mouth started to open, or it was missed. This time increased as fish developed.

The failure of the snap of a 14-mm pike larva on a *Daphnia* (Fig. 3a) was due only to the movements of the prey during the snap, since the aiming was very accurate; the ppud was very small. The speed of the centroid of the mouth aperture (Fig. 3c) is first mainly due to swimming, but later on increasingly to relative movements of the upper and lower jaws. The pike started to open its mouth at a distance of about 2 mm from the prey. The maximal acceleration of the prey was 5.2 m/s^2 and its maximal velocity 34 mm/s (Fig. 3b). Because only movements in the plane of projection were considered, all values are minimum estimates. Unfortunately, in this snap, no ventral view was made. At the end of the jump the centre of the prey was just in front of the upper jaw. The prey finally escaped with a second jump. The failure of the snap was only due to the movements of the prey. Maximal velocity of a prey during uptake by 12- to 15-mm pike larvae was 0.84 m/s (error 0.05 m/s) (the velocity of the suction flow was thus 60 body lengths (BL)/s; Fig. 4).

Suction Process of the Carp

While searching for prey, carp larvae (6–8 mm SL) swam intermittently. Periods of 80–160 ms of activity, consisting of about two beats of the pectoral fins, often accompanied with low-amplitude oscillations of the body, alternated with periods of rest (often 0.2–0.4 s, but also frequently much longer). The velocity during activity was several body lengths per second; during rest it was very low (less than 0.1 BL/s). After a burst of activity, larvae decelerated rapidly. A typical attack sequence lasted about 400 ms. Before snapping, the larvae fixed their prey by turning both eyes symmetrically forward. No real S-shaped attack posture occurred; only one or two vigorous half oscillations of the body were seen (see Fig. 5b) accompanied by vigorous movements of the pectoral fins. The pectoral fins became folded against the body and the opercular valve opened at the moment of actual prey intake. Possible explanations for this folding were that the outflow of water from the opercular slit would be hindered by spread out pectoral fins, the velocity of the fish at the moment of prey intake was maximized by a synchronization of the power stroke of the fins with prey intake, and it was the start of a gliding phase during which the drag should be minimized. Suction started when the mouth began to open. Increments of time were associated with the last film-frame that the mouth was closed. Maximal angular velocity of the length axis of the mouth cavity reached approximately 10°/ms during 5 ms (see Drost and van den Boogaart 1986b, fig. 2). This velocity was less than for the startle response in larval zebra fish where up to 20°/ms during 10 ms was recorded (Kimmel et al. 1980). The start of swimming preceded by about 10 ms the onset of suction. The prey entered the mouth 4–6 ms after the onset of suction, or it was missed. In some movies the prey could be seen moving inside the mouth cavity through the transparant walls of the oral cavity. The entrance of the esophagus was reached within 20 ms. The food entered the esophagus after about 1 s. The branchiostegal valve opened after about 8 ms, so the prey was captured with valves of the fishes still closed.

Sometimes the direction of the movement of the centre of the mouth aperture during a snap was almost perpendicular to the length axis of the mouth cavity (76° in Fig. 6). The prey did not make active movements during this snap. Maximal velocity of the prey at the time of capture by small carp larvae was 0.26 m/s (error 0.03 m/s) (so the larva created a suction current of 45 BL/s).

TABLE 2. Measured distance (mm) between the centre of the mouth aperture and the centre of mass of the prey. Positive values indicate that the centre of mass is above the centre (lateral view) or left of the centre (seen from above). Values are means ± SD (number of measurements). The mean is also called aiming target, and the standard deviation aiming inaccuracy.

	Vertical	Left–right
Pike 14 mm	−0.38±0.26 (5)	−0.12±0.30 (6)
Pike 62 mm	−0.18±0.72 (8)	−0.27±0.74 (8)
Carp 6–8 mm	−0.15±0.24 (9)	−0.01±0.20 (10)

Strike Accuracy

Vertical versus left–right ppuds for carp and small and large pike were not significantly different at the 5% level (Student's *t*-test) (Table 2). Contrary to my expectations, however, the vertical aiming target (=mean) differed significantly (5%) from the centre of the prey (=zero) for pike larvae. The difference was close to significant for small carp. Both fish species aimed too high so that the prey entered through the lower half of the mouth aperture. For pike juveniles the difference was very small and not significant. The left–right aiming target did not deviate significantly from the centre of mass of the prey. In all three cases there was no difference between vertical versus left–right aiming inaccuracies. During the ontogeny of pike, aiming inaccuracy increased from 0.28 mm at a length of 14 mm to 0.73 mm at a length of 62 mm. The aiming inaccuracy relative to the standard length decreased from 2 to 1.2%; larger pike aimed relatively better. Aiming inaccuracy of 6–8 mm carp larvae was 0.23 mm. The relative aiming inaccuracy of carp larvae (3.5%) was greater than that of pike.

Maximal mouth radius during prey intake increased from 0.25–0.30 mm for a 6-mm carp larva to 0.35–0.40 mm for an 8-mm carp larva. Thus, mean maximal mouth radius did not

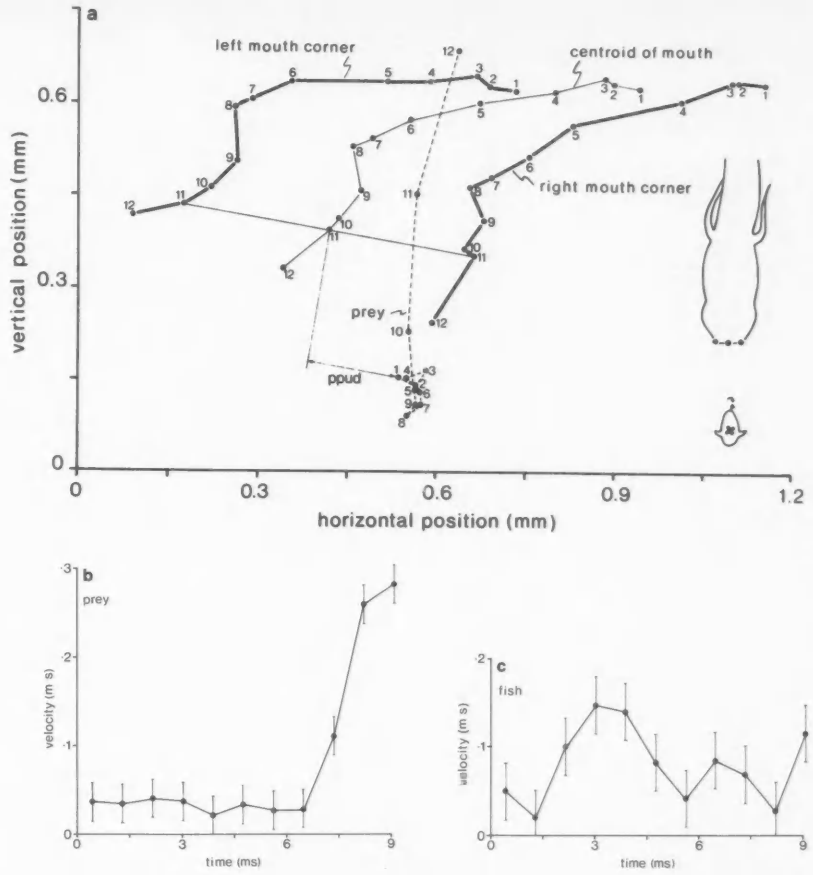

FIG. 6. Example of the suction act of a 5.8-mm carp larva feeding on an *Artemia* nauplius (traces from this very intensive feeding act are given in Drost and van den Boogaart 1986b). Film speed was 1150 fr/s. (a) Measured positions of left and right corner of the mouth and their middle and the position of the centroid of the prey in ventral projection. A small suction velocity towards the axis of the mouth cavity was visible. The movement of the centroid of the mouth was not parallel to the mouth axis, as we would expect in swimming, but almost perpendicular to it (76°). (b) Velocity of the prey. The prey was stationary first (velocity less than 0.04 m/s) and then sucked into the mouth cavity, with a maximal velocity of 0.26 m/s. (c) Velocity of the centre of the mouth aperture. This velocity showed no clear trend in time.

increase relative to the length of the larvae (4.6% at 6 mm; 4.7% at 8 mm). Mouth width was 0–20% larger than maximal mouth height. I combined the data of the 6- to 8-mm larvae to have more observations in one class.

Model Construction

The relationship between aiming inaccuracy and catch success with more or less spherical prey could be calculated with a mathematical model (Beyer 1980), using the following simplifying approximations: (1) the vertical and left–right ppuds were normally distributed, with a mean of zero and equal standard deviations; (2) vertical and left–right ppuds were independent; (3) the prey entered the mouth if the pud was less than the mouth radius (Fig. 7). The mouth aperture was considered to be circular, and parallel aiming was assumed optimal.

The following critical remarks about these assumptions could then be made.

(1) In principle, normality can be tested with the measured ppuds. However, I made too few measurements to test it. In the ventral views, the mean did not deviate from zero, but in the lateral view, carp and pike larvae aimed too high. The influence of nonzero mean on the calculated catch success is treated in the next section.

(2) The correlation between vertical and left–right ppud of the carp snaps was not significantly different from zero ($r^2 = 0.22$, $n = 9$, $p = 0.05$; Fig. 8). This correlation might result from a constant inaccuracy of the strike angle. Both ppuds were then correlated to the attack distance. A part of the measured correlation may have resulted from a correlation between length of the carp larva and both left–right and vertical ppuds. The number of observations is, however, rather low (nine). The influence of the parametric correlation on the

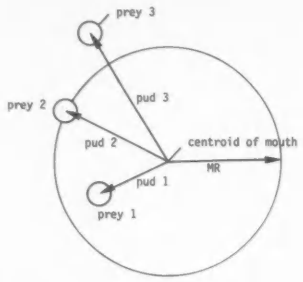

FIG. 7. For a successful attack in the model the perpendicular uptake distance (pud) must be less than the mouth radius (MR). Prey 1 will be taken in ($pud_1 < MR$); prey 3 will be missed ($pud_3 > MR$). Prey 2 is the boundary ($pud_2 = MR$).

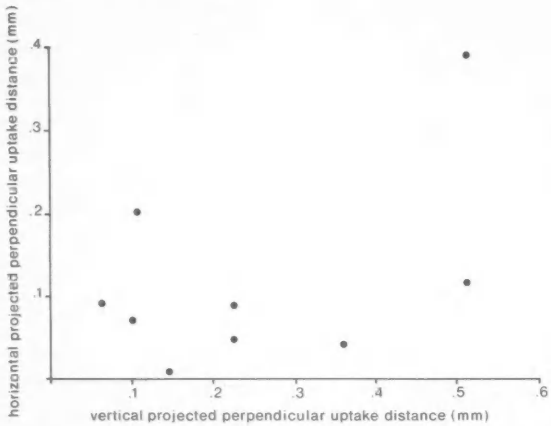

FIG. 8. Absolute values of vertical versus left–right ppuds in nine snaps of 6- to 8-mm carp larvae ($r = 0.47$, $p > 5\%$).

calculated catch success is given in the next section.

(3) During the suction process, water velocity has a radial component in the direction of the centre of the mouth. The relative magnitude of this radial component depends on the ratio between swimming velocity and suction velocity (Muller and Osse 1984; Muller and van Leeuwen 1985; Drost 1986). Therefore, a prey outside the mouth radius could be sucked in depending on the exact position of the dividing streamline, i.e. the streamline separating water that tends to flow into the mouth cavity from water than does not. In the model, however, sucking was treated similarly to filtering; thus, no prey more than one mouth radius from the length axis could be taken in. Although this condition is not fully fulfilled, this is assumed to have only a minor influence.

Although these three assumptions were only partly fulfilled, the deviations were small enough to continue with the model. Theoretically the frequency distributions of the vertical and the left–right ppuds are normal, the mean being the centre of the prey. A combination of the vertical and the left–right ppuds yielded a two-dimensional frequency distribution of the perpendicular uptake position (pup), i.e. the position of the centre of mass of the prey relative to the length axis. This distribution was a bivariate normal distribution. Starting from the frequency distribution of the pup, the frequency distribution of the pud (Fig. 9a) can be calculated as explained in Fig. 9b. The cumulative frequency distribution of the pud yielded the probability that the pud was less than a given value (Fig. 10). Assuming that the prey entered the mouth if the pud was less than the mouth radius, the expected catch success could be read directly on the ordinate of Fig. 10, while the ratio of mouth radius/aiming inaccuracy was put on the abscissa.

Aiming Inaccuracy: Comparison of Observed and Predicted Catch Success

Calculated and measured catch success were in the same order of magnitude (Fig. 10), as far as the low number of observations was concerned. Of the eight filmed snaps of larval pike, five were successful; in one the *Daphnia* escaped by a jump perpendicular to the suction (Fig. 3), in one the prey was just sucked in, but swam out of the mouth aperture a little later, and in one a larva missed a nonmoving prey. The observed catch success due to aiming was thus 87.5%; the calculated catch success was 80%. For the pike larvae, escape of the prey (*Daphnia*) caused more failures than bad aiming by the fish. The expected catch success of juvenile pike was 100%. Indeed all eight filmed snaps were successful. Catch success of 159 snaps of pike juveniles (60–70 mm) feeding on larval carp was also determined visually, i.e. without films. Of these snaps, 153 were successful (96.2%). Catch success for carp larvae was measured based on 18 snaps (78%). In eight snaps the magnification on the film was too low to measure the ppuds. Calculated catch success was 66%. I never saw *Artemia* perform escape movements. All failures were caused by bad aiming. Catch success was also determined visually for carp larvae feeding on *Artemia* nauplii. It increased from 51.2% for 5.7-mm larvae to 88.5% for 7.4-mm larvae.

The effect of a parametric correlation between vertical and left–right ppuds on the calculated catch success was rather low (Fig. 11a). At a medium correlation (0.5 as compared with the calculated value of 0.47 for small carp larvae; Fig. 8), the calculated catch success differed only slightly from the zero correlation. The calculated catch success was appreciably influenced at high values of parametric correlation only.

To determine the effect of a systematic deviation when aiming at the prey on the catch success, the vertical aiming target was varied, i.e. the fish aimed below or above the prey. An increase in the vertical aiming target from zero to 0.5 times the aiming inaccuracy had only a minor influence on the calculated catch success; a doubling of the aiming inaccuracy reduced the catch success appreciably (Fig. 11b). The measured vertical aiming target was about 0.5 times the aiming inaccuracy for the carp larvae and was greater than the aiming inaccuracy for 14-mm pike larvae (Table 2). The calculated catch success in Fig. 10 thus overestimated the catch success of carp and small pike larvae.

Influence of Prey Size on Catch Success

In my model the size of the prey had no influence on the calculated catch success; the prey was captured if the centre of mass was in front of the fishes mouth aperture. Beyer (1980) also regarded spheres and assumed that the prey was only ingested if even its outer margin was in front of the mouth aperture; thus, the size of the prey was important for catch success. To settle this problem, I have calculated from my raw data the expected catch success assuming Beyers "outer margin" condition. I have considered an *Artemia* nauplius to be a sphere with a radius of 0.1 mm. For carp the relative aiming

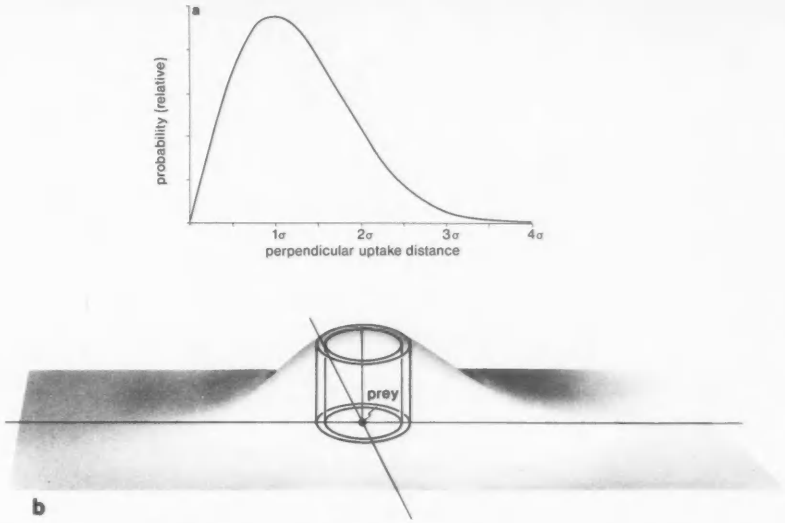

FIG. 9. (a) Theoretical probability density distribution of the pud, i.e. the distance between the centre of mass of the prey and the length axis. This distribution was calculated according to Fig. 9b. The distribution gives the probability that the pud has a certain value. (b) Theoretical probability density distribution of the pup. Total volume under the mound is 1. The probability that the pud is greater than r and smaller than $r + dr$ is given by the volume of the cylinder skin.

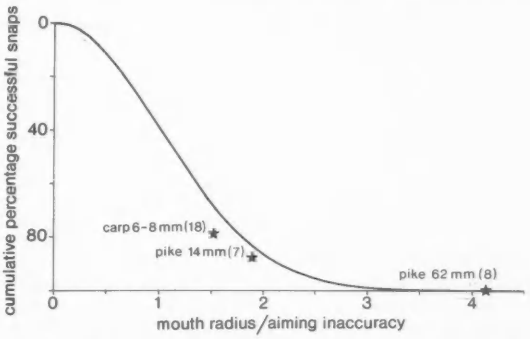

FIG. 10. Theoretical probability density distribution of the cumulative pud. It shows the probability that the pud is less than the given value. On the abscissa the ratio of maximal mouth radius/aiming inaccuracy is given; the ordinate gives the percentage successful snaps as calculated with the model. Observed catch success for pike and carp larvae measured with high-speed movies is indicated (number of observations in parentheses).

inaccuracy was then 92.5%. This corresponded to a catch success (Fig. 10) of 44%. The expected catch success in the first case (66%) was much closer to the observed catch success (78%). Therefore, the interpretation of my measurements using the model did not indicate a relationship between catch success and prey width for relatively small prey. Obviously, this would change when the prey width approached maximal mouth diameter. Catch success of anchovy larvae (age 17 d) dropped from 80 to 40% when the prey was changed from *Brachionus* (diameter 0.133 mm) to *Artemia* nauplii (diameter 0.236 mm) (Hunter 1972). Beyer (1980) explained this by the greater radius of the nauplii. My suggestion is that the larvae sucked faster toward the nauplii and that the increase in velocity caused an increase in aiming inaccuracy. To conclude, aiming inaccuracy should be measured with high-speed movies of larvae feeding on sluggish or on fast prey.

Parallel Aiming

The accuracy of parallel aiming was much more difficult to determine than the accuracy of perpendicular aiming. The inaccuracy of the latter was the distance between the centroid of the prey and the mouth, which was easily determined. To be able to measure parallel aiming accuracy, the optimal attack distance with given strike movements had to be known. van Leeuwen and Muller (1984) gave predictions for optimal movements of fish when sucking prey, based on theoretical considerations. Optimal strike distance could have been calculated from accurate motion curves of the mouth cavity (Drost and van den Boogaart (1986a), but this was laborious and the results were not accurate enough. However, bad parallel aiming might also cause unsuccessful snaps. This was not taken into account by my model.

Parallel aiming might be important. Most failures of largemouth bass (*Micropterus salmoides*) are caused by parallel aiming (Nyberg 1971), whereas most failures of hybrid tiger muskie (*Esox* sp.) are caused by perpendicular aiming (Webb and Skadsen 1980).

Influence of Escape Movements of Prey on Catch Success

Both aiming accurately (striking at the right place) and attacking fast (preventing the prey to escape) might be important in optimizing an attack. Some remarks on escape movements are given below, and a more extensive treatment is given in Drost (1986).

The movement required by the prey to avoid being sucked into the mouth cavity equalled the mouth radius of the larva

TABLE 3. Movement data for zooplankters. Measured maximal acceleration and distance covered. in the first 20 ms of the movement. Data are measured from multiflash photographs (escape of *Cyclops scutifer*) or high-speed films (other data).

Species	Maximal acceleration (m/s^2)	Distance covered (mm)	Movement type	Reference[b]
Copepoda				
Diaptomus franciscanus	15	2.25	Escape	1
Cyclops scutifer	12	0.74	Hop and sink swimming	2
C. scutifer	—	1 (in 5 ms)	Escape	3
Cladocera				
Daphnia pulex	6.5	0.8	Escape	1
Rotifera				
Polyarthra vulgaris	—	0.7[a]	Escape	4

[a]During the escape movement the velocity changed erratically. The distance covered is calculated from the mean velocity.

[b]References: 1, Lehman (1977); 2, Strickler (1977); 3, Strickler and Ball (1973); 4, Gilbert (1985).

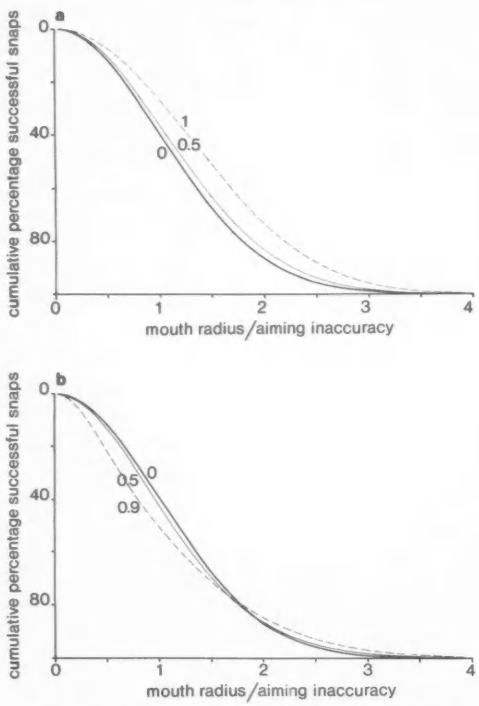

FIG. 11. Theoretical probability density distribution of the cumulative perpendicular uptake distance. The curves were constructed by sampling by computer 2×10^6 pairs out of a standard normal distribution. The standard deviation was always taken as 1; mean was 0 for the ventral view. The mean in the lateral view and the parametric correlation between vertical and left–right pudds could be varied. Pud was calculated using Pythagoras. The values were divided in 100 classes of width 0.04 times the aiming inaccuracy. (a) Different values for the parametric correlation between left–right and vertical ppuds: 0, 0.5, and 0.9; both means equal 0. (b) Different values for the vertical mean (aiming target). Parametric correlation was taken as 0.

under the following conditions: (1) the prey started to move perpendicular to the strike direction at the onset of the strike; this direction seemed to minimize the chance of being captured; (2) the aiming inaccuracy was zero, i.e. the predator aimed exactly at the centre of mass of the prey; (3) once started, the larva did not adjust its strike. The following remarks about these assumptions could be made.

(1) Some prey (species) jumped away before the snap started (e.g. calanoid copepods); others never jumped away (e.g. *Artemia* nauplii). Whether or not this condition is fulfilled depends on the species preyed upon.

(2) If the pup had a bivariate normal distribution, the distance required for the prey to come outside of the radius of the mouth aperture was a complex function. Taking the aiming inaccuracy as equal to zero greatly simplified the calculations.

(3) It was impossible to determine whether the larva has adjusted its strike axis to an escaping prey because the movement of the centroid of the mouth aperture followed a curved path, even if the prey did not try to escape. Lateral deflections were caused by swimming movements (see Fig. 5); vertical movements were caused by the asynchronous movements of upper and lower jaws. Given the short duration of the attack, it was reasonable to think that the movements were rather stereotyped once they had started (see also Nyberg 1971; Osse and Muller 1980).

For a 14-mm pike larva, maximal mouth radius was about 0.7 mm and strike time about 20 ms. Thus, *Diaptomus* and *Cylops* are well able to escape from a prey-sucking pike larva with speed, and *Daphnia* can barely do so (Table 3). The question whether aiming or speed is more important in increasing catch success during ontogeny is important for future research concerned with the relation between catch success and the rapidly changing morphology of fish larvae. If increase in speed was the most important factor, the changes in form during ontogeny might be regarded as hydrodynamical optimizations for a higher catch success. Hydrodynamical models as described by Muller et al. (1982) and van Leeuwen and Muller (1984) for adult fish and Drost (1986) for larval fish were useful to interpret the changes in morphology and kinematics during attack, optimizing the velocity of the prey. However, if the effects of aiming on catch success were the

most important, investigations should focus more on the improvement of the senses and muscular coordination during the ontogeny. From the present study, both aiming and speed seemed to be important.

Acknowledgements

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References

ARNOLD, G. P., AND P. B. N. NUTTALL-SMITH. 1974. Shadow cinematography of fish larvae. Mar. Biol. 28: 51–53.

BEYER, J. E. 1980. Feeding success of clupeoid fish larvae and stochastic thinking. Dana 1: 65–91.

BLAXTER, J. H. S. 1969. Development: eggs and larvae, p. 177–252. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Academic Press, New York, NY.

BLAXTER, J. H. S., AND M. E. STAINES. 1971. Food searching potential in marine fish larvae, p. 467–485. *In* D. J. Crisp [ed.] Fourth European Marine Biology Symposium. Cambridge University Press, Cambridge.

BRAUM, E. 1963. Die ersten Beutefanghandlungen junger Blaufelchen (*Coregonus wartmanni* Bloch) und Hechte (*Esox lucius* L.). Z. Tierpsychol. 20: 257–266.

1967. The survival of fish larvae with reference to their feeding behaviour and the food supply, p. 113–131. *In* S. D. Gerking [ed.] The biological basis of fish production. Blackwell Scientific Publishers, Oxford.

CHITTY, N. 1981. Behavioral observations of the feeding of the larvae of bay anchony, *Anchoa mitchilli*, and bigeye anchovy, *Anchoa lamprotaenia*. Rapp. P.-V. Reun. Cons. Explor. Mer 178: 320–321.

CONFER, J. L., AND P. I. BLADES. 1975. Omnivorous zooplankton and planktivorous fish. Limnol. Oceanogr. 20: 571–579.

DRENNER, R. W., R. STRICKLER, AND W., J. O'BRIEN. 1978. Capture probability: the role of zooplankter escape in selective feeding of planktivorous fish. J. Fish. Res. Board Can. 35: 1370–1373.

DROST, M. R. 1986. Models of prey capture in larval fish. Thesis, Agricultural University, Wageningen.

DROST, M. R., AND J. G. M. VAN DEN BOOGAART. 1986a. A simple method for measuring the changing volume of small biological objects, illustrated by studies of suction feeding by fish larvae and of shrinkage due to histological fixation. J. Zool. 206: 239–249.

1986b. The energetics of feeding strikes in larval carp (*Cyprinus carpio*). J. Fish. Biol. 29: 371–379.

GILBERT, J. J. 1985. Escape response of the rotifer *Polyarthra* a high speed cinematographic study. Oecologia (Berl.) 66: 322–331.

HUNTER, J. R. 1972. Swimming and feeding behaviour of larval anchovy *Engraulis mordax*. Fish. Bull. U.S. 70: 821–838.

1980. The feeding behavior and ecology of marine fish larvae, p. 287–330. *In* J. E. Bardach, J. J. Magnuson, R. C. May, and J. M. Reinhart [ed.] Fish behavior and its use in the capture and culture of fishes. ICLARM Conference Proceedings 5. ICLARM, Manilla, Philippines. 512 p.

KIMMEL, C. B., R. C. EATON, AND S. L. POWELL. 1980. Decreased fast start performance of zebrafish larvae lacking Mauthner neurons. J. Comp. Physiol. 140: 343–350.

LEHMAN, J. T. 1977. On calculating drag characteristics for decelerating zooplankton. Limnol. Oceanogr. 22: 170–172.

MEYER, A. 1986. First feeding success with two types of prey by the fry of the central American cichlid fish, *Cichlasoma managuense*, morphology and behavior. Environ. Biol. Fishes. (In press)

MILLS, E. L., J. L. CONFER, AND R. C. READY. 1984. Prey selection by young yellow perch: the influence of capture success, visual acuity and prey choice. Trans. Am. Fish. Soc. 113: 579–587.

MULLER, M., AND J. W. M. OSSE. 1984. Hydrodynamics of suction feeding in fish. Trans. Zool. Soc. Lond. 37: 51–135.

MULLER, M., J. W. M. OSSE, AND J. H. G. VERHAGEN. 1982. A quantitative hydrodynamical model of suction feeding in fish. J. Theor. Biol. 95: 49–79.

MULLER, M., AND J. L. VAN LEEUWEN. 1985. The flow in front of the mouth of a prey-capturing fish, p. 233–237. *In* H. R. Duncker and G. Fleisher. [ed.] Vertebrate morphology. Gustav Fisher Verlag. Stuttgart, New York, NY. Fortschritte der Zoologie 30.

NYBERG, D. W. 1971. Prey capture in the largemouth bass. Am. Midl. Nat. 86: 128–144.

OIESTAD, V. 1984. Predation on fish larvae as regulatory force, illustrated in mesocosm studies with large groups of larvae. NAFO Sci. Counc. Stud. 8: 25–32.

OSSE, J. W. M., AND M. MULLER. 1980. A model of suction feeding in teleostean fishes with some implications for ventillation, p. 335–352. *In* M. D. Ali [ed.] Environmental physiology of fishes. Nato-Asi Series A, Life Sciences. Plenum Publishing Corp., New York, NY.

STRICKLER, J. R. 1977. Swimming of planktonic *Cyclops* species (Copepoda, Crustacea): patterns, movements and their control, p. 599–613. *In* T. Y. T. Wu, C. J. Brokaw, and C. Brennen [ed.] Swimming and flying in nature (2). Plenum Press, New York and London. 917 p.

STRICKLER, J. R., AND A. K. BALL. 1973. Setae of the first antennae of the copepod *Cyclops scutifer* (Sars): their structure and importance. Proc. Natl. Acad. Sci. USA 70: 2656–2659.

VAN LEEUWEN, J. L. 1984. A quantitative study of flow in prey capture by the rainbow trout, *Salmo gairdneri*, with general consideration of the actinopterygian feeding mechanism. Trans. Zool. Soc. Lond. 37: 171–227.

VAN LEEUWEN, J. L., AND M. MULLER. 1984. Optimum sucking techniques for predatory fish. Trans. Zool;. Soc. Lond. 37: 137–169.

WEBB, P., AND J. M. SKADSEN. 1980. Strike tactics of *Esox*. Can. J. Zool. 58: 1462–1469.

WIGGINS, T. A., T. R. BENDER, V. A. MUDRAK, AND J. A. COLL. 1985. The development, feeding, growth and survival of cultured American Shad larvae through the transition from endogenous to exogenous nutrition. Prog. Fish-Cult. 47: 87–93.

WINFIELD, I. J., G. PEIRSON, M. CRYER, AND C. R. TOWNSEND. 1983. The behavioural basis of prey selection by underyearling bream (*Abramis brama* (L.)) and roach (*Rutilus rutilus* (L.)). Freshwater Biol. 13: 139–149.

Analysis of Mark–Recapture Data from Hatchery-Raised Salmon Using Log-Linear Models

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Green, P. E. J., and P. D. M. Macdonald. 1987. Analysis of mark–recapture data from hatchery-raised salmon using log-linear models. Can. J. Fish. Aquat. Sci. 44: 316–326.

Large numbers of hatchery-raised juvenile Pacific salmon are routinely marked with coded-wire tags before release from the hatchery. Log-linear models are an appropriate statistical technique to analyze the numbers of recaptures in different fisheries, and the numbers of tagged fish returning to the hatchery, in terms of such factors as brood year, treatment at the hatchery, timing of release, and size at release. Log-linear analysis of catches and hatchery returns of chinook salmon (*Oncorhynchus tshawytscha*) from Robertson Creek, British Columbia, indicates that all of these factors are important, but variation between brood years overrides all other factors. Within a brood year, the conditions that maximize the number of returns to the hatchery do not necessarily maximize the number of recaptures in the fishery. Log-linear analysis of hatchery returns from a designed experiment on a single brood year of coho salmon (*O. kisutch*) from Rosewall Creek, British Columbia, quantifies the effects of the various factors but will be of limited value until the causes of variations between brood years are better known.

Des étiquettes métalliques codées sont systématiquement fixées avant le lâcher à de grands nombres de saumons du Pacifique juvéniles d'élevage. Des modèles linéaires–logarithmiques constituent une technique statistique appropriée pour analyser le nombre de poissons recapturés au cours de différentes pêches et le nombre de poissons étiquetés qui reviennent à la piscifacture, du point de vue de facteurs comme l'année de génération, les traitements en piscifacture, le moment du lâcher et la taille au lâcher. L'analyse linéaire–logarithmique sur les prises et les retours aux piscifactures de saumon quinnat (*Oncorhynchus tshawytscha*) du ruisseau Robertson (Colombie-Britannique) révèle que tous ces facteurs sont importants, mais la variation entre les années de génération l'emporte sur tous les autres facteurs. Dans une année de génération, les conditions qui maximisent le nombre de saumons revenant à la piscifacture ne maximisent pas forcément le nombre de recaptures au cours de la pêche. Une analyse linéaire–logarithmique des retours aux piscifactures obtenue dans le cadre d'une expérience portant sur une seule année de génération du saumon coho (*O. kisutch*) fréquentant le ruisseau Rosewall (Colombie-Britannique) quantifie les incidences des divers facteurs; toutefois, cette analyse n'aura qu'une valeur limitée tant que les causes de la variation entre les années de génération ne seront pas mieux comprises.

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Many salmon hatcheries on the Pacific coast of Canada and the United States routinely carry out extensive coded-wire tagging operations before the young are released. Commercial fisheries, sports fisheries, and returning spawners are sampled for tags. The objectives of the coded-wire tagging program are to determine the survival rates, migration patterns, and contributions to different fisheries of the different stocks. This paper examines data from two hatcheries on Vancouver Island, the Robertson Creek hatchery and the Rosewall Creek hatchery.

In this paper, we address three management problems. First, we examine whether hatchery procedures can affect the ratio of Alaskan to Canadian catches. Second, we look at whether hatchery procedures can affect the number of fish returning to the hatchery. Finally, we compare the year-to-year variability to the hatchery-induced variability. To answer these questions we apply a class of log-linear models. We introduce log-linear models and discuss the statistical problems associated with them. For this type of mark–recovery data, they are seen as preferable to analysis in terms of the catch equation and also to conventional analysis of variance on untransformed counts. Log-linear models are then used to analyze data on chinook salmon (*Oncorhynchus tshawytscha*) released from the Robertson Creek hatchery in 1972–77 and coho salmon (*O. kisutch*) released from the Rosewall Creek hatchery in 1975. The Rosewall Creek experiment was designed by Bilton (1980) and originally analyzed by a response surface analysis (Bilton et al. 1982).

In a companion paper (Green 1987), chinook migration patterns were studied by graphical analyses of the Robertson Creek chinook data.

Methods

Fish are marked with coded-wire tags before they are released from the hatchery. They are sampled for tags at the end of their lives, either through recapture in the fishery or on their return to the hatchery to spawn. Their life cycle begins in the hatchery, where fertilized eggs from returning salmon are incubated for several months until hatching and the fry are reared in large ponds until ready for release. Some of the maturing fry are marked with a 1-mm coded-wire tag (CWT) implanted into the nose cartilage. The adipose fins of the tagged fish are clipped to permit their identification later.

The rearing fry are kept in different ponds. Some ponds are designated as "production", while others may be given special treatments such as experimental diets. All fish treated similarly have the same tag code. When a group of fish is released, the average weight and the release date are noted. The number of tagged fish released is known from counters on the tagging machines, while the number of untagged fish is estimated from egg inventory data.

After release, the fish migrate to the Pacific Ocean. Each fish will eventually suffer one of the following possible fates: it may return to the hatchery to spawn; it may spawn elsewhere; it may be caught by troll, net, or sports fishermen; or it may die of "natural" mortality. The main factors in "natural" mortality are disease and predation. The life span of these fish is at most 6 yr after fertilization. In this paper, the age of the fish is the number of calendar years after the year in which the eggs were fertilized (the brood year).

Every fish returning to the hatchery is examined for a clipped adipose fin. The commercial catches are also sampled for fish with clipped adipose fins. Tagged fish are measured and their heads sent to a dissection laboratory. The tags are excised from the nose cartilage and the code is read under a microscope.

The catches in the commercial fisheries are too large to permit examination of every fish. A proportion of the boats is sampled and the number of marks in a geographical region is inflated with an "expansion factor" which is the reciprocal of the sampling proportion (proportion of catch sampled) for that geographical region. The expanded number is calculated for biweekly or monthly time intervals. The statistical effects of expansion are considered later in this paper. The data for the sport fishery depend on fishermen voluntarily bringing in the heads of salmon with missing adipose fins to head depots. Since the proportion doing so is unknown, the sport catches cannot be expanded. It is estimated that sport fishing accounts for approximately 21% of the total chinook catch (Pearse 1982).

These coded-wire mark–recapture programs are different from other mark–recapture experiments in several respects. The most important difference is that the population size is known from the outset of the experiment, whereas in most mark–recapture experiments that is the parameter to be estimated. Sampling for coded-wire tags is destructive so there is no possibility of multiple recaptures. The marking is done only at age zero, which causes some problems when estimating survival rates (Brownie et al. 1978). Finally, virtually all of the marked and unmarked fish that escape both the fishery and natural mortality return, at the end of their lives, to their original point of release. In principle, all of the returning fish may be sampled; however, some of them spawn in the river below the hatchery; the proportion doing so is not known, and these fish escape sampling.

In this analysis we are studying the effects of auxiliary variables on recapture probabilities, in a fashion similar to Pollock et al. (1984). This is different from mark–recapture experiments in which the purpose is to estimate biologically meaningful parameters such as population size or survival rates, without considering auxiliary variables. In this modelling exercise, parameters are still estimated; however, these are estimates of the effects of the auxiliary variables.

Log-Linear Models

Models of the general class used in this paper are called log-linear models. They have the form

$$(1) \quad \vec{\pi} = e^{\vec{X}\vec{\beta}}$$

where $\vec{\pi}$ is an $n \times 1$ vector of probabilities, $\vec{X}$ is an $n \times p$ design matrix of full rank, and $\vec{\beta}$ is a $p \times 1$ vector of parameters. Exponentiation of a vector is defined as exponentiation element by element. The model is called "linear" because the term $\vec{X}\vec{\beta}$ is a linear function of the parameters. If, for example, one column of $\vec{X}$ is used for a covariable and another is used for its square, the model will allow for a quadratic response to that covariable, but it would still be called a linear model.

In this paper, the probabilities are probabilities of recapture for different categories of fish. The different categories correspond to different combinations of the factors of interest. The model can also be written $\vec{\mu} = E(\vec{Y}) = e^{\log(\vec{N}) + \vec{X}\vec{\beta}}$, where $\vec{Y}$ is an $n \times 1$ vector of random variables whose elements Y_i are the numbers of recaptures, $E(\vec{Y}) = \vec{\mu}$ is the vector of expected numbers of recaptures in the different categories, and $\vec{N}$ is an $n \times 1$ vector of the numbers of fish released from the hatchery. In the vector $\vec{N}$, each number of fish released may appear several times, once for each combination of factors under which that group was recaptured. The logarithm of a vector is defined by taking logarithms element by element. There is a column in the design matrix for each parameter in the model. The parameters in the vector $\vec{\beta}$, with the exception of the grand mean parameter, are called "effects." They measure the effects, on the baseline recapture probability, of different values of continuous auxiliary variables (covariables) such as weight at release, and different levels of categorical auxiliary variables (factors) such as treatment. The grand mean parameter is the logarithm of the baseline recapture probability. Interactions between categorical variables, and between categorical and continuous variables, may also be estimated. For more on this topic the reader is referred to Searle (1971) or McCullagh and Nelder (1983).

This class of models was chosen because the effects are combined multiplicatively. Multiplicative models, unlike additive models, cannot lead to negative expected counts. Bilton et al. (1982) fitted an additive model to untransformed counts and noted that the possibility of negative expected counts could be a problem.

The most suitable error distribution is Poisson; hence, the models can be treated as log-linear models. We can assume this here because the estimated probabilities of recapture are all less than 5%, so the extra complications of the hypergeometric distribution (Seber 1982) can be avoided. Log-linear models are easy to use with the computer package GLIM (Baker and

Nelder 1978). GLIM allows estimation of the parameters and fitting of the models by maximum likelihood. GLIM will handle data from unbalanced as well as balanced experimental designs and will determine if any parameters are aliased. By using GLIM we do not need to develop special computer programs for maximum-likelihood estimation of mark–recovery data, such as Conroy and Williams (1984) did. Conroy and Williams (1984) were primarily concerned with the estimation of survival rates, not the effects of auxiliary variables. Cormack (1981) has shown how GLIM can be used to estimate biological parameters from multiple mark–recapture data, again by the use of log-linear models. We also justified the use of log-linear models, at least for the continuous auxiliary variables, by plots which showed linear relationships between the logarithms of the recapture probabilities and the covariates weight and Julian day of release.

The model-fitting procedure is similar to that of stepwise regression. Parameters are entered into the model, by adding appropriate columns to the design matrix, and estimated by maximum likelihood. The goodness-of-fit of the model is then examined. The parameters are entered one at a time and in different sequences, since, in general, they are nonorthogonal. The parameters that cause large improvements in the goodness-of-fit are then included in the model and more are added subsequently. Only main effects are entered at first, followed by selected interactions. In this way, the most important auxiliary variables, those that most improve the fit of the model, are found. The data from Robertson Creek are inherently very messy (in the sense of, for example, Urquhart and Weeks 1978), since they do not come from a designed experiment. In the cross-classifications of the variables under study, there are many empty cells. Fitting high-order interactions leads to much aliasing and hence difficulty in interpreting the results. Fitting only main effects and low-order interactions leads to a more parsimonious model. The emphasis during model fitting is not so much to find a "best" model but rather to determine which sources contributed most to an improvement in the fit. This is done by examining reductions in "deviance", as explained below. Little emphasis is put on significance testing, since this is largely irrelevant when we are primarily interested in relative reductions in deviance. Furthermore, there are distributional uncertainties due to the expansion factors and overdispersion, also considered below, which would make suspect any calculation of a p-value. Salsburg (1985) criticized the use of significance testing as the sole tool of statistics, and we agree with his comments.

For a detailed discussion on how the goodness-of-fit of the models is examined, the reader is again referred to McCullagh and Nelder (1983, chap. 2). A brief description is given here to introduce the concept of "deviance."

Let y_i be the ith element in a vectory $\vec{y}$ of independent observations. A density function of the form

$$f_Y(y_i;\theta,\phi) = \exp\{((y_i\theta - b(\theta))/a(\phi)) + c(y_i,\phi)\}$$

is said to be a member of an exponential family of distributions for a known value of ϕ, given functions a, b, and c and some θ. The parameter ϕ is called the dispersion parameter. For the Poisson distribution, for example,

$$f_Y(y_i;\mu_i) = e^{-\mu_i}\mu_i^{y_i}/y_i!$$

where, in our case, $\mu_i = E(Y_i) = N_i \exp \sum_{j=1}^{p}\beta_j x_{ij}$, p being the number of parameters in the model and Y_i the random variable corresponding to the observed value y_i. The density function f_Y can be reexpressed in the exponential family form

$$f_Y(y_i;\theta_i,\phi) = \exp((y_i\theta_i - e^{\theta_i}) - \ln(y_i!))$$

where $\theta_i = \ln \mu_i$, $a(\phi) = 1$, $b(\theta_i) = e^{\theta_i}$, $c(y_i,\phi) = -\ln(y_i!)$ and $\phi = 1$. The general form of the log likelihood, considered to be a function of $\vec{\theta} = (\theta_1, \ldots, \theta_n)$ with the data vector $\vec{y} = (y_1, \ldots, y_n)$ being given, is written

$$(2)\quad l(\vec{\theta};\vec{y}) = \sum_i((y_i\theta_i - b(\theta_i))/a(\phi) + c(y_i,\phi)).$$

The deviance, expressed in terms of the mean value parameter $\vec{\mu}$ (McCullagh and Nelder 1983, p. 25), is defined as

$$(3)\quad \text{deviance} = -2(l(\vec{\mu};\vec{y}) - l(\vec{y};\vec{y}))$$

where $l(\vec{y};\vec{y})$ is the maximum log likelihood achievable for an exact fit in which fitted values equal the data (the "saturated" model). The deviance is a measure of the discrepancy of a fit. If we calculate the maximum-likelihood estimate of $\vec{\mu}$ for the current model and denote it $(\hat{\mu}_1, \ldots, \hat{\mu}_n)$, then for the Poisson distribution the deviance is

$$\text{deviance} = 2\Sigma(y_i\ln(y_i/\hat{\mu}_i) - (y_i - \hat{\mu}_i))$$

with summation over all categories. This is the statistic labelled G^2 by Bishop et al. (1975) with $a(\phi) = 1$. It is also equivalent to the likelihood ratio statistic and is distributed asymptotically as a chi-square random variable (Bishop et al. 1975, chap. 14). The deviance is equivalent to $2\Sigma y_i\ln(y_i/\hat{\mu}_i)$, since $\Sigma(y_i - \hat{\mu}_i) = 0$. Deviance is a general term describing the discrepancy of a fit. For the normal distribution the deviance is the familiar residual sum of squares.

There are three special considerations for the present application. The first is the effect of the expansion factors. The number of recaptures found in the sampled boats is multiplied by an expansion factor to give an estimate of the total number of recaptures in the catch. This use of an expansion factor means that the choice of the function $a(\phi) = 1$ in the exponential model will cause the variance to be underestimated. To see this, let Y_s be the number of sampled recaptures, Y the total number of recaptures, both sampled and unsampled, and f the sampling fraction. Then Y_s/f is the estimate of Y. If we assume that Y_s is distributed as a Poisson random variable with mean μ_s and that Y is Poisson with mean μ, then $\mu_s = f\mu$ and

$$E(Y_s) = \mu_s,\ \mathrm{Var}(Y_s) = \mu_s$$
$$E(Y) = \mu,\ \mathrm{Var}(Y) = \mu.$$

If we expand the sampled recaptures by the sampling fraction (the inverse of the expansion factor), then $E(Y_s/f) = \mu_s/f = \mu$ but

$$(4)\quad \mathrm{Var}(Y_s/f) = \mu_s/f^2 = \mu/f.$$

However, the assumption of Poisson errors implies that

$$E(Y_s/f) = \mathrm{Var}(Y_s/f) = \mu.$$

Comparing this with (4) shows that the Poisson assumption will underestimate the variance of the expanded recaptures. To correct this, we can set

$$(5)\quad a(\phi) = \phi/f$$

by use of a weighting vector during model fitting with GLIM. During fitting it is sufficient to set $\phi = 1$; then ϕ can be estimated by

$$\hat{\phi} = G^2/(n-p)$$

when a satisfactory fit is found (McCullagh and Nelder 1983, p. 133). Using (5) with $\phi = 1$, we have

$$\text{Var}(Y/f) = \mu a(\phi) = \mu/f$$

which agrees with (4). The deviance will be decreased by the use of (5) as we can see by examining (2) and (3).

The second consideration is the problem of overdispersion relative to the model of Poisson variation, i.e. $\text{Var}(Y/f) > \mu/f$. This indicates that $\phi > 1$. This can occur if the observations are not independent, which would happen, for example, if the marked fish were in any way clumped together. Since ϕ can be estimated from the data, we can estimate the amount of overdispersion. If there is overdispersion, we cannot assume a Poisson distribution but will assume that the data are distributed as a scaled Poisson.

The estimate of the dispersion parameter can be used for testing. If there are two models whose deviances we denote G_1^2 and G_2^2, then an approximate chi-square statistic for testing whether the second model offers a significant improvement over the first can be calculated from

$$\{(G_1^2 - G_2^2)/(p_2 - p_1)\}\,(\hat{\phi}_2)^{-1}$$

where p_i is the number of parameters fitted in model i ($i = 1, 2$), $p_2 > p_1$, all the parameters of the first model are included in the second, and $\hat{\phi}_2 = G_2^2/(n - p_2)$. This is analogous to an F-test using error sums of squares for two models to test whether the second significantly improves the fit. The estimate of dispersion is given in the analysis of deviance tables because it is a good measure of the goodness-of-fit. The smaller the dispersion, the better the fit, or the less unexplained deviance.

The third consideration is the method by which the initial population size vector $\vec{N}$ is treated during model fitting. Taking logarithms of the log-linear model gives

$$\log(E(\vec{Y})) = \log(\vec{N}) + \vec{X}\vec{\beta}.$$

We do not wish to estimate $\log(\vec{N})$, since it is a known vector of constants whose regression coefficient is known to be 1. By specifying that it is an "offset" in GLIM terminology, it is subtracted from the log-transformed data and the result regressed on the remaining covariates (Baker and Nelder 1978).

The log-linear models presented in this paper are proposed as an alternative to models for commercial mark–recapture data based on the "catch equation", that is

$$N_t = N_0\, e^{-(F+M)t}$$

where N_t is the number of individuals remaining after t time intervals from the initial population size N_0 and F and M are the instantaneous coefficients of fishing and natural mortality, respectively. Using the catch equation, it can be shown that

$$\pi_i = \frac{F_i}{F_i + M_i}\left\{\exp\left(-\sum_{j=1}^{i-1}(F_j + M_j)\right)\right\} \times \left\{1 - \exp(-(F_i + M_i))\right\}$$

where π_i is the probability of recapture in time period i and the subscripts on F and M denote the fact that they vary with time. This approach has been used by Nicholson and Pope (1977) and Gulland (1955), for example, and is described in Seber (1982). In this paper we are not relating the recapture probabilities to F and M, but to a set of auxiliary variables. In any case, F and M are not separately estimable. In the data set under study there is no information on natural mortality. The total natural mortality can be estimated but it is not possible to estimate the M_i, as the times of death are not known. There is no way to estimate F_i unless values for the M_i are assumed. The context in which they are being assumed, with or without fishing mortality, must be made clear. As Lawless (1982, p. 491) pointed out, estimating the hazard function that would result if other causes of death were removed requires strong assmptions. Furthermore, fishing mortality is clearly age and time dependent because of the type of gear used in the troll fishery. There may also be mortalities due to fishing that are not observed as fishing mortality and would hence be incorrectly classified as natural mortalities. Examples are damage to fish that escape or predation by seals or sea lions while on the hook (Ricker 1976). Thus "natural mortality" could be different at different fishing mortalities.

On the other hand, by excluding F and M from the models in our analysis, our conclusions cannot be extrapolated to different fishing strategies or to changes in management techniques or to conditions under which a component of natural mortality not modelled by any of the auxiliary variables may change.

Chinook Salmon from the Robertson Creek Hatchery

The data set consists of 20 tag-code groups from brood years 1972–77 (Table 1). In their raw form, the recapture data are given by month for 12 regions along the Pacific coast, ranging from Oregon State to the top of the Alaskan Panhandle (Fig. 1), for all years in which the salmon were caught by the three types of fishing gear. The hatchery-return data include only the total number of returns of each CWT group per year. No information on fishing effort was available to us. The average weight refers to the average weight of a sample of fish taken from the CWT group at the time of release.

The treatments EWOS and OMP in Table 1 refer to two different food types; however, some sources say that groups 2 and 3 were production groups, that is, grown under the usual, nonexperimental conditions. As such, two classifications of treatments were established for model fitting. The first, denoted T_1, places groups 2 and 3 with the production groups and thus has five levels; the second, denoted T, considers them to be separate treatments, and thus has seven levels. Groups 13–18 were designated as "early", "mid", or "late" release time. This factor is similar to the Julian day of release, but not quite the same. For example, the "mid" treatment group in 1976 (No. 17 in Table 1) was released on the same Julian day as the "early" treatment group in 1975 (No. 15). A measure of incubation and pond rearing time would be more useful than the day of release, since the "ideal" day of release probably depends on many factors, such as degree-days accumulated, which vary from year to year. Unfortunately, the hatchery managers could not provide us with this information.

Groups 5 and 12 were not included in many of the analyses because they were found to be too unusual due to their very high and low release weights, respectively.

Analysis of Fishery Recaptures

This was an attempt to model the response (number of recaptures) in Alaska and British Columbia as a function of various effects and covariables. The model was of the log-linear form (1). The factors or effects modelled were age at recapture (A),

TABLE 1. Description of the coded wire tag groups (Robertson Creek).

Group No.	Tag code	Treatment	Release weight	Tagged release	Total release	Release day	Brood year
1	02/05/01	Production	5.7	26 881	510 739	129	1972
2	02/08/01	EWOS	5.5	2 627	2 627	171	1972
3	02/11/01	OMP	5.4	39 013	222 819	171	1972
4	02/02/03	Production	5.9	23 480	603 717	191	1973
5	02/08/06	Supersmolt	41.3	20 777	73 094	448	1973
6	02/06/02	Production	5.0	16 137	29 352	172	1973
7	02/05/06	Production	6.3	27 726	520 930	196	1973
8	02/04/06	Production	6.3	27 444	438 094	191	1973
9	02/06/06	Production	5.2	46 194	1 003 877	162	1974
10	02/09/06	Production	5.3	27 383	453 766	162	1974
11	02/12/06	Production	4.5	11 674	11 674	158	1974
12	02/14/06	Production	2.7	28 283	228 940	162	1974
13	02/04/09	Late	5.2	47 724	462 985	162	1975
14	02/04/08	Mid	5.2	50 731	487 145	155	1975
15	02/13/05	Early	5.4	10 702	10 829	146	1975
16	02/16/29	Early	5.3	59 227	63 054	130	1976
17	02/16/30	Mid	5.4	64 550	3 188 072	146	1976
18	02/16/31	Late	5.3	69 203	442 487	159	1976
19	02/22/17	Production	4.4	70 816	4 178 531	156	1977
20	02/22/18	Production	5.3	66 725	3 553 187	154	1977
Total				737 297	16 485 919		

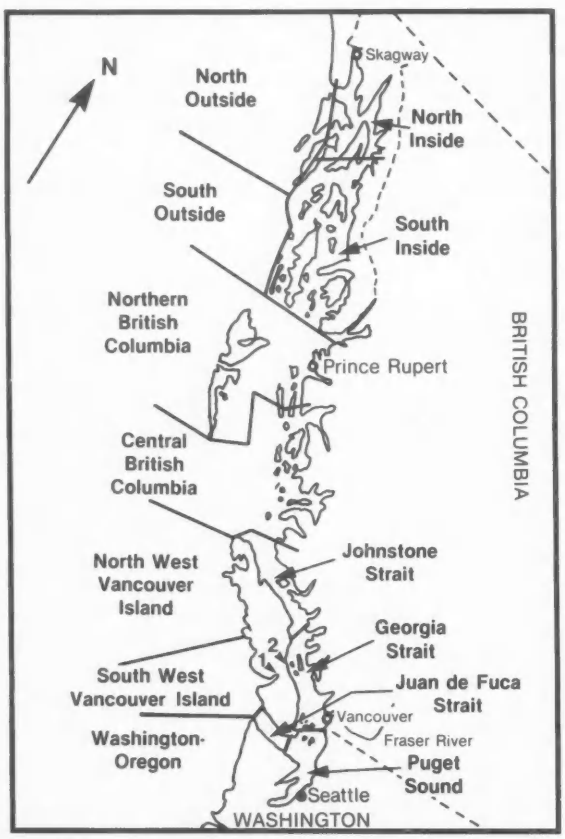

FIG. 1. Commercial catch regions for the Pacific coast. 1 = Robertson Creek Hatchery, 2 = Rosewall Creek Hatchery.

prerelease treatment (T or T_1), brood year (B), and place of recapture (R). Place of recapture was characterized as 12 different locations (Fig. 1), without taking into account the geographical relationships between the statistical areas. The covariables were weight at release (W) and Julian day of release (J).

A model that includes all the main effects could be written out in full as

$$(6)\quad E(Y_{hijkl}) = N_{hjk}\exp(\omega + \alpha_i + \tau_j + \xi_k + \gamma_l + \theta_1 W_{hjk} + \theta_2 J_{hjk})$$

where ω is the grand mean, α_i is the effect due to age at recapture i, τ_j is the effect due to treatment j, ξ_k is the effect due to brood year k, γ_l is the effect due to the place of recapture l, and θ_1 and θ_2 are the slopes of the log observations versus the two covariables. The index h indicates the release group. The number of recaptures, Y_{hijkl}, is assumed to be distributed as a scaled Poisson with expected value $E(Y_{hijkl})$. In terms of the general log-linear model notation (1), parameters ω, the α's, the τ's, the ξ's, the γ's and θ_1 and θ_2 are successive elements in the vector β. The nonzero N_{hjk}'s are successive elements in the vector $\vec{N}$.

Before fitting was begun we did some preliminary plots and calculations which showed that the ratio of recaptures in Alaska to those in British Columbia varied considerably over the lifetimes of the fish (Table 2). No age 2 fish were recaptured in Alaska and very few in British Columbia. Generally, more age 3 fish were caught in British Columbia than in Alaska, but for ages 4 and 5 this ratio was reversed. Hardly any age 6 fish were caught in either place. The age 2 fish are small, have a low commercial value, and are not caught in large quantities. The age 6 fish have a higher commercial value but are not numerous in the fishery or elsewhere. For these reasons, only ages 3–5 were included in the model.

A weighting vector for GLIM was defined by taking the reciprocal of the sampling fraction for each recapture group. The sampling fractions for yearly totals were known for most

TABLE 2. Alaska/British Columbia recapture ratios by age (troll fishery) (BC = fish caught only in British Columbia; AL = fish caught only in Alaska).

Group	Age 2	Age 3	Age 4	Age 5	Age 6
1		0.31	BC	5.14	
2		BC	1.55	2.23	AL
3		0.35	0.67	3.33	AL
4		0.05	0.83	1.67	
5		BC	0.93	0.67	
6		0.12	2.00	AL	
7		0.11	3.38	1.77	
8		BC	0.44	0.60	0.67
9	BC	0.49	1.23	2.95	
10		0.53	1.13	3.92	
11		0.39	0.84	AL	
12	BC	1.25	1.67	2.00	
13	BC	0.28	1.14	1.15	
14	BC	0.19	1.27	2.18	
15		0.24	3.00	2.00	
16	BC	0.35	0.99	3.86	
17	BC	0.26	1.04	1.23	
18	BC	1.15	1.79	1.79	
19		0.09	1.80	2.86	
20		0.63	1.79	5.33	

of the CWT groups at the three ages and two locations. Where they were not known, the mean sampling fraction was used.

The importance of an auxiliary variable or interaction is indicated by its relative reduction in deviance (Table 3). Model 2 is the simplest and includes only main effects. The reduction in deviance achieved by adding brood year shows that there are very large differences in the recapture rates for different brood years. These differences are greater than those due to the different treatments. The reduction in deviance obtained with the second classification of the treatments is much larger than that obtained using T_1, so the food pellets that CWT groups 2 and 3 were given had some effect on the recapture rates. CWT group 2 showed a greater recapture rate than group 3, which was less than, but quite close to, that of the production groups. Treatment 6 ("mid" release time) produced the most recaptures.

Model 6 shows that there is an important interaction between age at recapture and place of recapture (Table 3). This confirms the tendency, noted above, for the British Columbia fishery to exploit the younger fish (age 3), while the Alaskan fishery exploits ages 4 and 5.

Models 7 and 8 show that Julian day of release has a stronger effect than weight at release on the recapture rates. Model 9 fits individual slopes for recapture rates against weight at release and Julian day of release, for each age at recapture and each place of recapture. All the slopes for Julian day are negative when it is entered first, except for age 5 in British Columbia for which it is positive. This suggests that as Julian day of release is increased, recaptures in British Columbia increase, while recaptures in Alaska decrease. When the release weights are added to the model, this difference in slopes disappears; however, a similar relationship appears for the release weights, indicating that as release weights rise, recaptures increase slightly faster in British Columbia than in Alaska. Note, however, that this applies over the range of release weights and Julian days observed in this data set, and the relations will not necessarily hold true when extrapolated.

Models 11–15 examine some of the interactions. It appears from these models that the interaction of brood year with age at recapture is important and the other interactions much less so, since $\hat{\phi}$ is smallest for those models which include that interactions.

The most important result from this analysis is the large reduction in deviance achieved by adding the brood year effect. This could mean that there are large yearly changes in fishing effort, in the genetics of the broods, in conditions at the hatchery such as water quality, in water level in the rivers leading to the ocean, in mortality after marking, and possibly other factors as well.

The differences in recapture rates in Alaska and British Columbia due to release weight and Julian day are in fact slight and it is doubtful whether it is worth trying to manipulate these in at attempt to increase recaptures in British Columbia. It is difficult to interpret the increasing recaptures due to increasing Julian day in the light of the fact that "mid" release time (treatment 6) was found to increase recaptures more than "early" or "late" release (treatments 5 and 7).

The large deviances in the anodev table can be misleading. Deviance is a measure of discrepancy between the fitted and observed values. Any model is an idealization and, except for the case of a saturated model where the number of fitted parameters equals the number of observations, there will always be a discrepancy between the fitted model and the observed data. With large sample sizes this discrepancy is almost certain to be detected by a statistical test, even though it may be small for practical purposes. Considerations of parsimony suggest that it is not desirable to add many more parameters solely for the purpose of reducing the goodness-of-fit to a statistically insignificant level, as the resulting model would be too complicated to interpret and, typically, the standard errors of the fitted parameters would be too large for the fitted model to be useful. What is needed is a measure of whether the discrepancy between observed and expected values is small enough that the fitted model can safely be used for prediction. This is not so much a statistical problem as a management one. How much of a discrepancy, or error, between predicted and observed values is acceptable from a management point of view?

The models presented here, or other related models, could be used to predict the catch of stocks of salmon in different locations. A model could be adapted to fit the requirements of fishery managers; for example, they may wish to have predicted catches broken down into smaller geographical regions. Confidence intervals could be constructed for the predictions, as is done in the next section. Since it is not possible to know what the brood year effect is until after the entire brood is dead; or until we learn the causes of the brood year effect, the manager could be asked to select between optimistic and pessimistic scenarios, and brood year effects would be chosen based on experience with previous estimates in former year-classes. This model would be more credible for predicting catches than would a simulation model that is not based on parameters estimated from data. Of course, the dangers of extrapolation remain.

Analysis of Hatchery Returns

In order for the hatchery to increase the number of salmon at sea and available for the fisheries, the hatchery managers must know the factors that affect the probabilities of capture. Are these the same factors that influence the number of salmon returning to the hatchery? By analyzing the hatchery-return data we can attempt to answer this question.

When the migrating salmon return to the hatchery at ma-

TABLE 3. Analysis of deviance for Robertson Creek recapture model. The symbols for the factors are as follows (combinations indicate interactions): M = grand mean, A = age at recapture, R = place of recapture, B = brood year, T_1 = treatments (first classification), T = treatments (second classification), J = Julian day of release (counted from January 1 and taking leap years into account), W = mean weight at release.

Model	Main effects	First-order interactions	Second-order interactions	Deviance	df	$\hat{\phi}$
1	M			3223	107	30.1
2	M,A,R			2147	104	20.6
3	M,A,R,B			1096	99	11.1
4	M,A,R,B,T_1			1055	97	10.9
5	M,A,R,B,T			767	95	8.1
6	M,A,R,B,T	AR		462	93	5.0
7	M,A,R,B,T,J	AR,AJ,RJ	ARJ	365	87	4.2
8	M,A,R,B,T,W	AR,AW,RW	ARW	378	87	4.4
9	M,A,R,B,T	AR,AW,RW,AJ				
	J,W	RJ	ARW,ARJ	314	81	3.9
10	M,A,R,B,T	AR,BA,AW,RW				
	J,W	AJ,RJ	ARW,ARJ	182	71	2.6
11	M,A,R,B,T	AR,BA,TA				
	J,W	AW,RW,AJ,RJ	ARW,ARJ	172	63	2.7
12	M,A,R,B,T	AR,BA,TA				
	J,W	AW,RW,AJ,RJ,BR	ARW,ARJ,BAR	111	48	2.3
13	M,A,R,B,T	AR,BR				
	J,W	AW,RW,AJ,RJ	ARW,ARJ	286	76	3.8
14	M,A,R,B,T	AR,TA				
	J,W	AW,RW,AJ,RJ	ARW,ARJ	239	71	3.4
15	M,A,R,B,T	AR,BA,AW				
		RW,AJ,RJ,BR	ARW,ARJ,BAR	119	56	2.1

turity, all of them are sampled. There are no expansion factors, no variable fishing effort, and so the statistical problems encountered in the previous section are avoided. The major problem encountered in analyzing these data is that not all of the fish that return to spawn return to the hatchery; many spawn in the river below the hatchery, and nothing is known about the proportion doing so. Factors affecting the number spawning below the hatchery could include water conditions and crowding at the hatchery entrance.

The factors that we may wish to include in a model for these data are the ages of the returning fish, their brood year, the year in which they returned, and the prerelease treatment. The effect of the average release weight and Julian day of release should also be included. Obviously, age at return and brood year will be aliased with the return year, since return year is the sum of age at return plus brood year. This means that there is no way of estimating, separately from age at return and brood year effects, the effects due to water conditions and other factors in the year that the fish return.

The data set consists of four returning age groups for the same 20 CWT groups described earlier. The two anomalous CWT groups were omitted from this analysis, leaving a total of 72 observed cases. The number of observations is quickly exceeded by the number of parameters when the interactions are fitted (well before the saturated model is reached) and there is much aliasing, especially between brood year and treatments. In particular, treatment 4 is aliased with the other treatments and treatment 7 is aliased with the 1976 brood year. When the brood year by treatment interaction is fitted, for example (model 20 of Table 4), there are an additional 30 parameters entered into the design matrix of model 4 to get model 20, but 28 of these are aliased. Thus, the degrees of freedom decline by only 2, from 59 to 57. This forces us to look for a very parsimonious model. With four return ages, six brood years, and seven treatments, there are a total of 168 possible categories. Less than 72 of these have data in them, since some have replicate observations. With such messy data, we should not be surprised if we cannot find a model which adequately explains the underlying mechanisms. The emphasis should be on trying to find effects that contribute a relatively large amount to the reduction in deviance, as in the previous section.

We are modelling in the log-linear form the probability of a fish returning to the hatchery. The treatments are those of the second classification of treatments, T, used in the recapture model. Model 4 includes main effects only, all of which significantly reduce the deviance (Table 4). Models 5 and 6 show that Julian day of release is, by a small margin, more important than weight at release as a covariable, if the slope is assumed to be the same in each response category.

Models 7–12 examine reductions in deviance obtained by fitting different slopes for the two covariables at each of the three main effects. None of these models are clear "winners." In all cases, Julian day of release causes a greater reduction in deviance than does weight at release, especially in interaction with age at return.

Models 13–15, 16–19, and 20–22 fit first-order interactions between different pairs of main effects and a different slope for either Julian day of release or release weight at each level of these interactions. It is not possible to fit any more interactions than this due to the structure of the data. While in some cases there may appear to be enough degrees of freedom remaining to fit another interaction, the interaction will usually be aliased with parameters already in the model. Hence, model 21 turns out to be identical to model 9, so nothing was gained by fitting the additional interactions. Similarly, model 22 is

TABLE 4. Analysis of deviance for Robertson Creek hatchery return model. The symbols for the factors are as follows (combinations indicate interactions): M = grand mean, A = age at return, B = brood year, T = treatments (second classification), J = Julian day of release, W = mean weight at release. Interactions shown in lowercase are completely aliased with other terms and may be omitted from the model without affecting the fit.

Model	Main effects	First-order interactions	Second-order interactions	Deviance	df	No. of parameters aliased	$\hat{\phi}$
1	M			5115	71	—	72.0
2	M,A			3309	68	—	48.7
3	M,A,B			1349	63	—	21.4
4	M,A,B,T			1113	59	2	18.9
5	M,A,B,T,W			1081	58	2	18.6
6	M,A,B,T,J			994	58	2	17.1
7	M,A,B,T,W	AW		929	55	2	16.9
8	M,A,B,T,J	AJ		851	55	2	15.5
9	M,A,B,T,W	BW		1007	54	3	18.7
10	M,A,B,T,J	BJ		1002	55	4	18.2
11	M,A,B,T,W	TW		1024	56	6	18.3
12	M,A,B,T,J	TJ		980	56	6	17.5
13	M,A,B,T	BA		601	44	2	13.7
14	M,A,B,T,W	BA,BW,AW	BAW	417	22	3	17.3
15	M,A,B,T,J	BA,BJ,AJ	BAJ	239	21	3	11.4
16	M,A,B,T	TA		868	44	5	19.7
17	M,A,B,T,W	TA,AW,TW	TAW	515	29	18	17.8
18	M,A,B,T,J	TA,AJ,TJ	TAJ	533	29	18	18.4
19	M,A,B,T J,W	TA,TW,tj AW,AJ	TAW,taj	398	25	42	15.9
20	M,A,B,T	BT		1050	57	30	18.4
21	M,A,B,T,W	bt,BW,tw	btw	1007	54	69	18.7
22	M,A,B,T,J	BT,BJ,TJ	btj	979	54	69	18.1

nearly identical to model 12. The model with the lowest dispersion and deviance and the most unaliased parameters is model 15. Model 14 is also quite good.

These two models show that including either release weight or Julian day of release with the interaction between brood year and return age improves the fit over that of a model which fits a common slope. Inclusion of Julian day of release causes the greatest improvement. The hatchery managers are well aware that weight and time of release are very important in determining the number that return. These analyses show that weight and time of release have different effects depending on the brood year and on the age of the fish that return. Even though these effects may appear to be slight, accounting for all of these differences does improve the overall ability of the model to predict returns.

Again the modelling effort shows that differences between brood years are very significant and emphasizes the need for further research on the causes of these differences. Bilton et al. (1982) analyzed the influence of time and size at release of juvenile coho salmon on returns at maturity to Rosewall Creek by using a response surface analysis. However, the entire experiment was carried out for only one brood. While a certain combination of size and time at release may produce high returns within a given brood, the differences in returns between broods might completely overshadow any gains obtained by manipulating hatchery conditions. The fact that brood year has such a strong effect in both hatchery-return data and fishery-recapture data shows that if it is fishing effort that causes the brood year effect, then fishing must kill a high enough proportion of the fish that there are significantly fewer fish available for spawning in the hatchery. If variations of effort in the troll fishery cause the observed brood year effect in the recapture models, then the terminal fishery (which operates in Alberni Inlet just before the salmon migrate up the Somass River to Robertson Creek) could contribute to the brood year effect in the hatchery-return models (Schnute and Sibert 1983). Terminal fishery catches could be built into this model. There are also sport and Indian fisheries but no data are available for these. It seems to us that a matter of utmost importance is to have reliable data on the effort in each fishery. Without these data it is impossible to determine whether there are factors other than fishing that influence both recaptures and returns, and, given the strength of the brood year effect, this is a serious gap in our understanding of the resource.

The sign of the slopes of the returns with respect to the two covariables at different brood years was examined (Table 5). It is striking that in brood year 1972 the estimates of the slopes are all greater than or equal to zero, whereas in brood year 1975 they are all less than or equal to zero. If two researchers had done separate mark–recapture experiments in these years, they would have reached opposite conclusions! This indicates that the value of the experiment of Bilton et al. (1982) will not be realized until it is repeated in other years.

Model 15 is used to demonstrate the use of this type of model for predicting returns (Fig. 2). This model (or a similar one) could be used to determine if there was a differential mortality between marked and unmarked fish. The model estimates the percentage of returning marked fish. It could similarly be used to predict the percentage of returning unmarked fish. By making these predictions for several years' releases, the total number of fish returning to the hatchery each year could be estimated. If these predicted numbers were consistently lower than

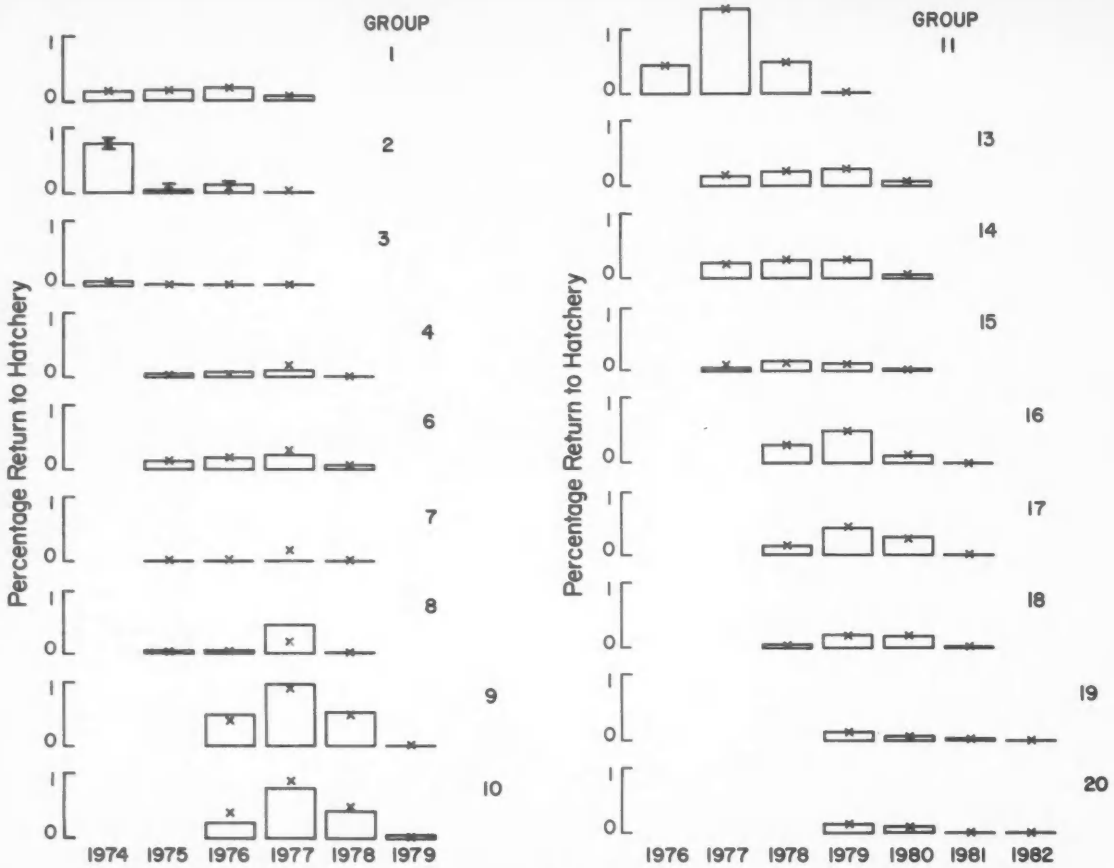

FIG. 2. Observed and estimated percentage returns from the Robertson Creek hatchery return model (model 15, Table 4). The bars represent the observed percentage returns for a given group of fish. The crosses show the returns estimated by the log-linear model. In most cases the range of the 95% confidence intervals on the model estimates was narrower than the width of the crosses; when the confidence intervals were large enough, they were plotted as horizontal lines above and below the crosses. The five bars are for ages 2–5. They are offset to show the effects of calendar years. The scale of the plots is shown in percentage points along the left. This figure shows that the model is quite accurate at estimating the observed values, even though the confidence intervals on some occasions do not overlap with the observed percentage returns. The difference between estimated and observed returns in these cases is only a fraction of a percentage point.

TABLE 5. Slopes of responses to covariables weight (W) and Julian day (J) for hatchery-return model (+ = positive slope, − = negative slope, 0 = not significantly different from zero, A = aliased, cannot be estimated).

	Age 2		Age 3		Age 4		Age 5	
Broodyear	W	J	W	J	W	J	W	J
1972	A	+	+	0	+	0	+	A
1973	−	−	0	−	0	0	0	−
1974	0	0	0	−	0	0	0	0
1975	−	0	−	0	−	0	−	0
1976	0	0	0	0	+	0	0	0
1977	0	0	0	0	0	0	A	0

the observed numbers, this would be an indication of greater mortality for marked fish.

The plot of estimated and observed values for model 15 (Fig. 2) is useful for demonstrating the close fit of the model to the data. The confidence limits of the estimated returns do not always include the observed number of returning fish. The difference is generally only a small fraction of a percentage point, which for practical purposes, and given the messiness of the data, is quite tolerable. If data were available on the sex of the returning fish, the fit could be improved, since males and females do not return to the hatchery at the same ages in the same proportions. There are virtually no 2- or 3-yr-old females returning to the hatchery, and no 5-yr-old males.

Coho Salmon from the Rosewall Creek Hatchery

We used log-linear models to reanalyze a set of data previously analyzed by Bilton et al. (1982). They used a response surface analysis to analyze the influence of time and size at release of coho salmon on their returns at maturity to Rosewall Creek. The data set consisted of six pond populations, three size groups (small, medium and large), and four release dates, giving a 6 × 4 × 3 factorial design. The release dates were

TABLE 6. Analysis of deviance for Rosewall Creek hatchery returns. The symbols for the factors are as follows (combinations indicate interactions): M = grand mean, A = age at return, P = rearing pond, J = Julian day of release, W = mean weight at release.

Model	Main effects	First-order interactions	Second-order interactions	Deviance	df	$\hat{\phi}$
1	M			3703	111	33.4
2	M,A			3286	110	29.9
3	M,J			2076	108	19.2
4	M,P			3639	106	34.3
5	M,A,J			1659	107	15.5
6	M,A,P			3223	105	30.7
7	M,J,P			2026	103	19.7
8	M,A,J,P			1610	102	15.8
9	M,A,J,P,W			1412	101	14.0
10	M,A,J,P,W	AJ		1246	98	12.7
11	M,A,J,P,W	JP		1348	91	14.8
12	M,A,J,P,W	AW		941	100	9.4
13	M,A,J,P,W	JW		1354	98	13.8
14	M,A,J,P,W	PW		1408	96	14.7
15	M,A,J,W	AJ,AW,JW	AJW	333	96	3.5
16	M,A,J,P,W	AJ,AW,JW	AJW	311	91	3.4

Julian days 104, 132, 161, and 189, all in the year 1975. On Julian day 189 there was only one pond population released. If the size groups were considered levels of a factor, the design would be nested, as all three size groups increased with the day of release. Since the average weight at release of each tag group was known, we treated weight as a covariable. Bilton et al. (1982) modelled both weight and Julian day as covariables, but we have treated Julian day as a factor. This gives a 6×4 design with five empty cells and three replicates in all other cells. Bilton (1980) gave a complete description of the data set.

Bilton et al. (1982) analyzed the sum of the hatchery returns and the commercial and sport catches of adult coho salmon, but only hatchery-return data for jacks (males that mature early at age 2). They assumed that the effects of time and size at release were additive and that errors were normally distributed and additive. Their model was nonlinear and consisted of eight unknown parameters which had no simple biological interpretation. One problem with their model was the assumption of normally distributed errors. As the authors stated, with this assumption the predicted responses could take physically impossible negative values. The effects were also entered additively, even though this is not recommended for count data (Bishop et al. 1975, p. 23–24). There were four release dates. They treated Julian day of release as a continuous covariable but it is treated here as a four-level factor, since the data were already grouped. This has advantages in estimating interactions.

Only the hatchery returns were modelled, as there were no data available on the expansion factors for sampling of the fishery. Adding the hatchery returns to the commercial and sport catches could have implications for the variance structure of the data. As discussed earlier, the variance and probability distribution of the commercial catches are affected by the expansion factors used, whereas the hatchery returns are not. How should the data be weighted when part of the count is expanded and part is not? There is a more fundamental reason for not adding the two counts: do the catches and returns really respond in the same way or should separate modelling attempts be made, as in this paper?

The factors included in our models were rearing pond (P), Julian day of release (J), and age at return (A). The age factor was used to differentiate between jacks and adults. The only covariable was release weight (W).

Analysis of Hatchery Returns

Two of the main effects, age at return and Julian day of release, were significant, irrespective of their order of entry into the model (Table 6). For practical purposes it is not worth including the pond effect; the six different pond populations contribute relatively little to reducing the deviance, although in a strictly statistical sense the reduction is significant, assuming the reduction in deviance to be distributed as a chi-square random variable.

Amongst the first-order interactions not involving the covariable weight at release, the interaction between age at return and Julian day of release is the strongest. Amongst those involving release weight, the interaction between age at return and release weight is the strongest. However, adding the second-order interaction between return age, Julian day, and release weight drastically reduces the deviance. Models 15 and 16 are proposed as suitable fits. The return age by Julian day terms are intercepts, and the return age by Julian day by release weight terms are slopes, for the logarithms of the returns as a function of release weight at each combination of return age and Julian day of release. Plots of the log returns against release weight showed that a linear relationship existed for all the return age by Julian day combinations. This relationship was strongest for the jacks. Correlations of log jack returns versus release weight for each Julian day were as high as 0.89. These plots and the estimates of the parameters from the models showed that the return of jacks is an increasing function of weight at release whereas the return of adults is a decreasing function. Moreover, there is some tendency for the slopes to approach zero at the later Julian days.

This implies that greater returns of jacks may be obtained by early release of larger juveniles, exactly as Bilton et al. (1982) found. In the case of adults, the maximum predicted returns are obtained by late release of small juveniles. This is contrary to the predictions of Bilton et al. (1982), probably due to the inclusion of commercial and sport catches in their analysis.

This may also explain why they found quadratic rather than linear relationships. The proportion of adult coho caught in the fisheries is about 5–10 times greater than the proportion returning to the hatchery. Thus, the factors maximizing hatchery returns are masked by those maximizing catches, and the same conditions will not maximize both.

Discussion

The analysis of the Robertson Creek chinook data was an attempt to use statistical models to extract as much information as possible about the effects of hatchery manipulations, from what was, in a statistical sense, an unplanned experiment. Because production from the hatchery could not be jeopardized, only minor variants from established procedures and a limited number of different combinations of variants could be tried. As a result, aliasing limited the complexity of models that could be fitted. Also, our findings cannot be extrapolated to conditions vastly different from normal production. Nonetheless, something was learned from the analysis.

The analyses of the Robertson Creek recaptures and returns show that the hatchery-induced variability is small compared with the variability between brood years. This implies that, within reasonable limits, there is little a hatchery manager can do to affect the recaptures and returns of fish until the factors causing the brood year variability are understood better. The analyses also established that the conditions which maximize returns to the hatchery will not necessarily be the same conditions which maximize catches in the fishery.

The experiment at Rosewall Creek was well designed using classical experimental design concepts. However, it was carried out only for one brood year. The Robertson Creek analyses showed that yearly variations are very large and there may be interactions between brood years and the other factors. This means that extrapolation of the results of the model developed here, or the model of Bilton et al. (1982), to predict the returns and/or catches of coho salmon in later years may give poor predictions. Manipulation of hatchery conditions based on these models could even decrease rather than increase the returns and catches for some brood years. Bilton et al. (1982) did some comparisons of their results with those from other hatcheries in Washington State and British Columbia and found a poor correspondence. They concluded that other as yet unrecognized factors may be influencing the results. We agree, and again emphasize the need for further research to determine what these factors are.

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References

BAKER, R. J., AND J. A. NELDER. 1978. The GLIM system, Release 3, Generalized linear interactive modelling. Numerical Algorithms Group, Oxford, U.K.

BILTON, H. T. 1980. Returns of adult coho salmon in relation to mean size and time at release of juveniles to the catch and the escapement. Can. Tech. Rep. Fish. Aquat. Sci. 941: 41 p.

BILTON, H. T., D. F. ALDERDICE, AND J. T. SCHNUTE. 1982. Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. Can. J. Fish. Aquat. Sci. 39: 426–447.

BISHOP, Y. M. M., S. E. FIENBERG, AND P. W. HOLLAND. 1975. Discrete multivariate analysis: theory and practice. MIT Press, Cambridge, MA. 557 p.

BROWNIE, C., D. R. ANDERSON, K. P. BURNHAM, AND D. S. ROBSON. 1978. Statistical inference from band-recoverey data: a handbook. U.S. Fish Wildl. Serv. Resour. Publ. No. 131: 212 p.

CONROY, M. J., AND B. K. WILLIAMS. 1984. A general methodology for maximum likelihood inference from band-recovery data. Biometrics 40: 739–748.

CORMACK, R. M. 1981. Loglinear models for capture–recapture experiments on open populations, p. 197–215. *In* R. W. Hiorns and D. Cooke [ed.] The mathematical theory of the dynamics of biological populations II. Academic Press, London.

GREEN, P. E. J. 1987. New graphical techniques for analyzing salmon migration in mark–recapture experiments. Can. J. Fish. Aquat. Sci. 44: 327–336.

GULLAND, J. A. 1955. On the estimation of population parameters from marked numbers. Biometrika 42: 269–270.

LAWLESS, J. F. 1982. Statistical models and methods for lifetime data. Wiley, New York, NY. 580 p.

MCCULLAGH, P., AND J. A. NELDER. 1983. Generalized linear models. Chapman and Hall, London. 261 p.

NICHOLSON, M. D., AND J. A. POPE. 1977. The estimation of mortality from capture–recapture experiments, p. 77–85. *In* J. H. Steele [ed.] Fisheries mathematics. Academic Press, London.

PEARSE, P. H. 1982. Turning the tide. A new policy for Canada's Pacific fisheries. The Commission on Pacific Fisheries Policy, Final Report. Department of Supply and Services, Ottawa, Ont.

POLLOCK , K. H., J. E. HINES, AND J. D. NICHOLS. 1984. The use of auxiliary variables in capture–recapture and removal experiments. Biometrics 40: 329–340.

RICKER, W. E. 1976. Review of the rate of growth and mortality of Pacific salmon in salt water, and noncatch mortality caused by fishing. J. Fish. Res. Board Can. 33: 1483–1524.

SALSBURG, D. S. 1985. The religion of statistics as practiced in medical journals. Am. Stat. 39: 220–223.

SCHNUTE, J., AND J. SIBERT. 1983. The salmon terminal fishery: a practical, comprehensive timing model. Can. J. Fish. Aquat. Sci. 40: 835–853.

SEARLE, S. R. 1971. Linear models. John Wiley, New York, NY. 532 p.

SEBER, G. A. F. 1982. The estimation of animal abundance and related parameters. 2nd ed. Macmillan, New York, NY. 654 p.

URQUHART, N. S., AND D. L. WEEKS. 1978. Linear models in messy data: some problems and alternatives. Biometrics 34: 696–705.

New Graphical Techniques for Analyzing Salmon Migration in Mark–Recapture Experiments

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Green, P. E. J. 1987. New graphical techniques for analyzing salmon migration in mark–recapture experiments. Can. J. Fish. Aquat. Sci. 44: 327–336.

New graphical techniques are applied to study the migration of chinook salmon (*Onchorynchus tshawytscha*). The techniques are based on plots of median recapture dates, log of the number of recaptures, and drawings of fish on grid maps. Under certain assumptions, the graphs can be used to generate hypotheses about the direction of movement of the salmon at different ages and brood years. The techniques developed are shown to adhere to the established principles of graphical design and could be extended for other similar studies.

De nouvelles techniques graphiques sont appliquées à l'étude de la migration du saumon quinnat (*Oncorhynchus tshawytscha*). Ces techniques sont basées sur des graphiques des dates médianes de recaptures, du logarithme du nombre de recaptures et des dessins de poissons sur des cartes quadrillées. En fonction de certaines hypothèses, les graphiques peuvent être utilisés pour élaborer des hypothèses sur la direction de la migration du saumon à différents âges et de différentes années de génération. On montre que les techniques mises au point observent les principes établis de conception graphique et peuvent être appliquées à d'autres études semblables.

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The purpose of this paper is to develop new graphical techniques to study migration in salmon mark–recapture experiments. The techniques are applied to the data from a large-scale coded-wire tagging mark–recapture experiment from the Robertson Creek hatchery on Vancouver Island. Many of the methods used to study migration have involved experiments where salmon are individually marked and recovered a short time afterwards. In contrast, this data set involves salmon which were marked in large numbers and recovered in commercial catches up and down the west coast of North America over a period of several years after release.

The paper out of necessity deals with two problems in parallel: statistical and biological. The statistical problem is to present a complex data set in such a way that irrelevant noise is filtered out without masking unexpected patterns. The biological problem is to generate new hypotheses relating to the migration of chinook salmon (*Onchorynchus tshawytscha*) by using the statistical techniques. Median recapture dates are shown to be useful in studying the direction of movement. A discussion of tables, mathematical models, and graphical techniques shows that graphical techniques are the most appropriate method of presenting both the median recapture dates and fish length information in this case. These techniques are developed and evaluated using the principles of graphical design of Bertin (1967, 1981), Tufte (1983), and Chambers et al. (1983). The graphs are discussed in terms of their graphical quality and as a tool for data analysis. Finally, several hypotheses about migration are generated to demonstrate their use.

The Data

The data, which are described in a companion paper (Green and Macdonald 1987), were not specifically collected for the purpose of studying migration. They do not contain any directional information, that is, there is no information on the direction of movement at the time of recapture. The data are inherently very messy; this is partly because of the observational nature of the study, partly because of the nature of the observations themselves, and partly because the study was not designed according to statistical principles of experimental or survey design. The data analyzed in this paper consist of the number, month and year, average length, and location of recapture for 20 groups of chinook salmon tagged with coded-wire tags between 1972 and 1977 and released from the Robertson Creek hatchery on Vancouver Island (Green and Macdonald 1987, fig. 1). The locations consist of 12 regions, or statistical areas, along the west coast of North America. The data are divided into two separate sets, one for each of the commercial gear types, troll and net.

Median Recapture Dates

Median recapture dates can be calculated and used to infer the direction of movement, despite the absence of directional information, under certain assumptions. The median recapture date is the date by which half a given group of fish were caught. The recapture date is taken as the number of days since January 1 of each year. A series of increasing median recapture dates along a series of points on a geographical axis could

indicate one of three things: first, that the fish radiated outwards from some origin not on the axis, arriving at close points first and distant points later; second, that the fish were moving in the direction of the increasing median recapture dates along the axis; third, that the observed squares are artifacts due to random variation. A final possibility is that the fishing effort was applied at successively later times during which the fish were equally available at all points. However, no data are available with which to refute or support this possibility.

The third possibility, that is, that the observed median recapture dates are merely random deviations from equal median recapture dates, was eliminated by doing a Kruskal–Wallis test of the hypothesis that the medians were all equal. This test returned a p-value of zero for both the troll and net data sets. The troll data set consists of 10381 fish (expanded, as explained in Green and Macdonald 1987).

The first possibility is a dispersion-type model of migration, discussed by Saila and Shappy (1963), Nicholson and Pope (1977), Quinn and Groot (1984), and others reviewed by Harden Jones (1968). Quinn and Groot (1984) have recently argued that many of the original assumptions of Saila and Shappy (1963) are incorrect in the case of Pacific salmon. They suggested that it is unlikely that Pacific salmon follow a dispersion-type migration.

The second possibility appears to be the most probable, and if we assume it to be correct, we can deduce the direction of movement of the salmon from the median recapture dates. Any series of increasing median recapture dates indicates that the salmon were probably migrating from the locations with the early median recapture dates to the locations with the later median recapture dates.

How should the median recapture dates be studied in order to find patterns relating to the movement of salmon? One possibility would be to tabulate the data in a well-organized manner. Tables are useful for answering questions at a fairly elementary level, by looking up one or two values, for example, and for small data sets. Here, we need to compare relative numbers of recaptures or median recapture dates with other variables, and as such, qualitative rather than quantitative answers are needed. The reading of tables for qualitative answers is very slow. For example, in comparing two tables of 10 rows by 10 columns, 200 individual instants of perception would be necessary for one combination of pairs of numbers out of thousands of possible combinations. In a graph, the perception would be more or less instantaneous (Bertin 1967, p. 7). Chambers et al. (1983, p. 179) emphasized that when a qualitative variable is portrayed, one should use a coding scheme which conveys magnitudes graphically, since numbers do not have the graded visual impact and are poor for this purpose.

Another option would be to develop a mathematical model which describes possible patterns of movement and to compare the median recapture dates with this model. A statistical test could then be carried out to examine the fit of the data to the mathematical model. However, to build such a model we would first have to examine the data graphically. In a complex data set such as this it would be extremely difficult, if not impossible, to design a model which could quantify our visual interpretation. It is sensible to use graphical analyses to check whether a mathematical model is appropriate. A mathematical model can only be used to check a visual interpretation if the visual interpretation is easily quantified, as in a linear relationship in a scatter plot. This is because the model and concomitant test must be designed to ask very specific questions. The visual interpretations are more appropriately tested with new experiments, but they are most appropriately found by using a graphical technique which filters out extraneous noise but not unexpected patterns.

The most reasonable approach is therefore to design a graphical tool to analyze these data. The tool should be specific enough for the data set in question, and general enough that it can be adapted to other situations. In this paper, I present graphical displays of the median recapture dates and other variables which foster the generation of hypotheses regarding the migration of Robertson Creek chinook salmon. The graphs have as their principal objective the detection of interesting patterns and the generation of hypotheses to explain them. Jacob (1981) made a similar point about the objectives of a graph: to help an observer guess at hypotheses about the data, rather than to present conclusions in a conventional or convincing fashion. The analysis of the graphs will be guided by the following five general questions: (1) How good is the information content of the data? (2) Where are the fish caught and how does this vary with the brood year and age? (3) In what direction are the salmon moving during the fishing season and how does this vary with their age and brood year? (4) How do the numbers of recaptures compare across geographical regions and according to age and brood year? (5) How do the sizes of recaptured salmon compare across geographical regions?

Building the Graphs

A good graphical display permits a data analyst to judge fully the quality of the information contained in a data set (Bertin 1967, p. 8). The problem is to construct good graphical displays. In order to construct a good graph, it is necessary to analyze fully the structure of the data to be graphed, the function(s) of the graph, and the components and information to be included in the graph. The recapture dates, recapture numbers, and size at recapture all vary with respect to the location of recapture, the age of the fish, and the brood year. Since location is described by two variables on a map (longitude and latitude), any display of the variables date, number, or size will have to be with respect to four other variables, for a total of five graphical components in the graph, as opposed to two in a scatter plot.

It is necessary to include all five graphical components in the graph. This is due to the level of the questions being asked. At the elementary level, questions deal with single elements of graphical components, such as a question asking for the median recapture date for a given brood year, location, and age. At the intermediate level, questions deal with subsets of elements of graphical components, such as a question comparing median recapture dates over a set of locations at ages 3 and 4 for all brood years. At the overall level, questions deal with entire components, such as whether median recapture dates change with location (see Bertin 1967, p. 141, or Bertin 1981, p. 12, for more details). With the exception of question 2, the questions are all at the overall level. If we wish to formulate questions including several components, then it is clearly advantageous to include all the components in the graph. If, for example, we wished to make comparisons between gear types, that is troll or net fisheries, then we would probably want to add gear type as a component to the graph.

There are two possible constructions for displaying the age/

brood year combinations of a variable on a map. This first is to construct one map per combination and the second is to superimpose all combinations on the same map. The first option is particularly useful in this data set where the combinations are ordered, since they are temporal. The latter option would make it more difficult to answer questions 2–5. To use the former option the geographical information will have to be displayed repetitively, but it is not necessary to display all the fjords and islands on the coast. The recapture data do not contain that level of resolution, since the statistical areas of the Department of Fisheries and Oceans are quite large (Green and Macdonald 1987, fig. 1). Therefore, the graph should contain only enough information to relate the different geographical regions approximately. This is consistent with the suggestion of Chambers et al. (1983, p. 326) that the gross structure of a graph be removed once it has been identified. This removes its domineering influence and can help us see finer structure or subtler effects. It also reduces the clutter of the graph. Bertin (1981, p. 144) gave examples of how maps may be simplified and is a strong proponent of the "collection of maps" idea. Royce et al. (1968, fig. 5) displayed similar data by using the second option, which resulted in a very confusing graph because it is impossible to detect overall patterns for a given variable.

The simplification of the geographical information is done by representing fig. 1 of Green and Macdonald (1987) in the form of the array shown in Fig. 1. This is similar to the "grid" or "mesh" maps of Bertin (1981, p. 144). The cells of the array are positioned relative to each other in approximately the same way as on the map (Green and Macdonald 1987, fig. 1). The recapture data are plotted in the cells of this array. To remove excess ink and clutter, the lines delineating the cells are removed. The exact geographical location of a cell, if desired, can be determined by counting positions in the array, or by making an acetate template. With a little practice, however, it becomes quite easy to remember and spot the correspondence.

In order to display graphically the actual recapture data in the cells of this array, squares are plotted whose dimensions are proportional to the magnitude of the data. Alternatively, some sort of mark could be plotted and its value (darkness), texture, colour, orientation, or shape varied (Bertin 1967, p. 9). Squares gave the best visual impact in trials of some of the alternatives. These squares are contrary to the principle of Tufte (1983, p. 57) that the number of information-carrying (variable) dimensions (of the mark) should not exceed the number of dimensions of the data. This would mean that we should plot some sort of line. In this case this principle is explicitly broken because we wish to compare the size of squares to other squares above, below, and to the left and right of each other, which is easier to do if both sides of the square vary. This may introduce a lie factor to the data (Tufte 1983, p. 57). A lie factor is the size of an effect shown in the graphic divided by the size of the effect in the data. To reduce this the log of the number of recaptures is used. The bottom left-hand corner of each square is always plotted in the same position. In Fig. 4 and 5 the largest squares represent 800 and 450 recaptured fish, respectively. Squares whose sides are less than half the dimensions of the corresponding cells in the array (Fig. 1) represent less than 20 and 15 recaptured fish, respectively. When only one fish is reported, squares are not drawn.

Hartigan and Kleiner (1984) introduced the concept of "mosaics" for graphical displays, but in a somewhat different sense. I use the word here because the overall appearance of a collection of squares and rectangles resembles the tiles in a mosaic.

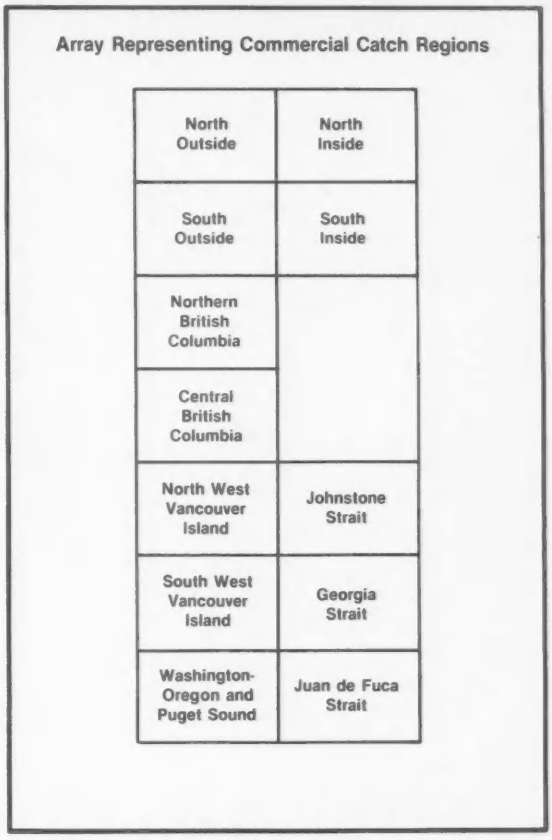

FIG. 1. Array representation of the commercial catch regions shown in Green and Macdonald (1987, fig. 1). The array is structured so that the relative position of each catch region is approximately the same as in the original geographical arrangement.

At first sight the mosaics (Fig. 2–5) may appear too complex. To examine whether or not this is so, we need to define the term in the visual context. Dondis (1973, p. 113) defined complexity as a visual intricacy made up of many elemental units and forces that results in a difficult process of organizing the meaning in the pattern, whereas simplicity is a visual technique of directions and singleness of elemental form, free from secondary complication or elaboration. These mosaics are designed to be free from secondary complications and elaboration, and have only two elemental forms (squares and rectangles). Their purpose is to achieve the clear portrayal of complexity, or the revelation of the complex (Tufte 1983, p. 191). The complexity in these mosaics is introduced by the data, not by the graphical design.

To restrict statistical graphics to plots with a pair of axes and plotted variables with clear-cut physical interpretations is desirable in many situations but would prevent us from using graphs for their most important analytical and exploratory uses. For these uses, a graph must be regarded first and foremost as a picture, and only secondarily as something with

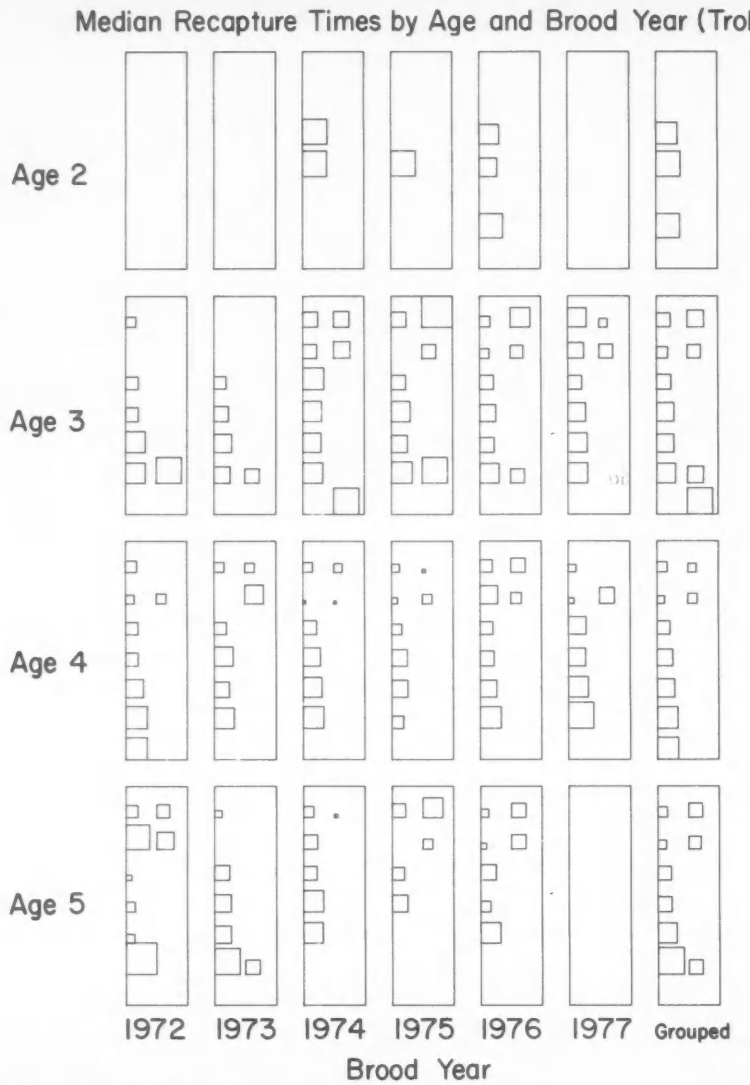

FIG. 2. Mosaics for combinations of brood years and ages using the median recapture times for the troll fishery as the response variable. The mosaics on the extreme right are calculated by grouping the data for the brood years 1972–77 before calculating the median recapture dates. See text for more detail.

axes (Chambers et al. 1983, p. 319). The qualitative nature of the answers in this study eliminates the requirement for axes giving actual numerical values, thereby simplifying the graph. What should be considered is the "mental cost" involved in understanding a graph (Bertin 1967, p. 12). Thus, rather than considering whether a graph is inherently complex, the primary criterion for evaluating a graph should be whether there is another graphical representation of the data which requires a lower mental cost.

Graphs of smiling and frowning fish were developed in order to answer question 5 (Fig. 6 and 7). These fish plots were suggested by the faces of Chernoff (1973) and Flury and Riedwyl (1981). The advantage of their faces is that they give a more attractive impression than other symbols; people like to look at them (Flury and Riedwyl 1981). The principle of the faces is that their features are varied (e.g. length of mouth and nose) to represent values of multivariate data. In question 5 we are attempting to study the morphometrics of the recaptured fish. It seemed natural to choose a symbol to do this which would enhance the data analyst's ability to detect and comprehend important phenomena and remember major conclusions (Chernoff 1973). The average length in a given location is represented by varying the length of the fish in the plot. The log of the number of fish used to determine the average length is represented by the smile of the fish. Any fish drawn with a straight face or a frown corresponds to a sample size of 25 or

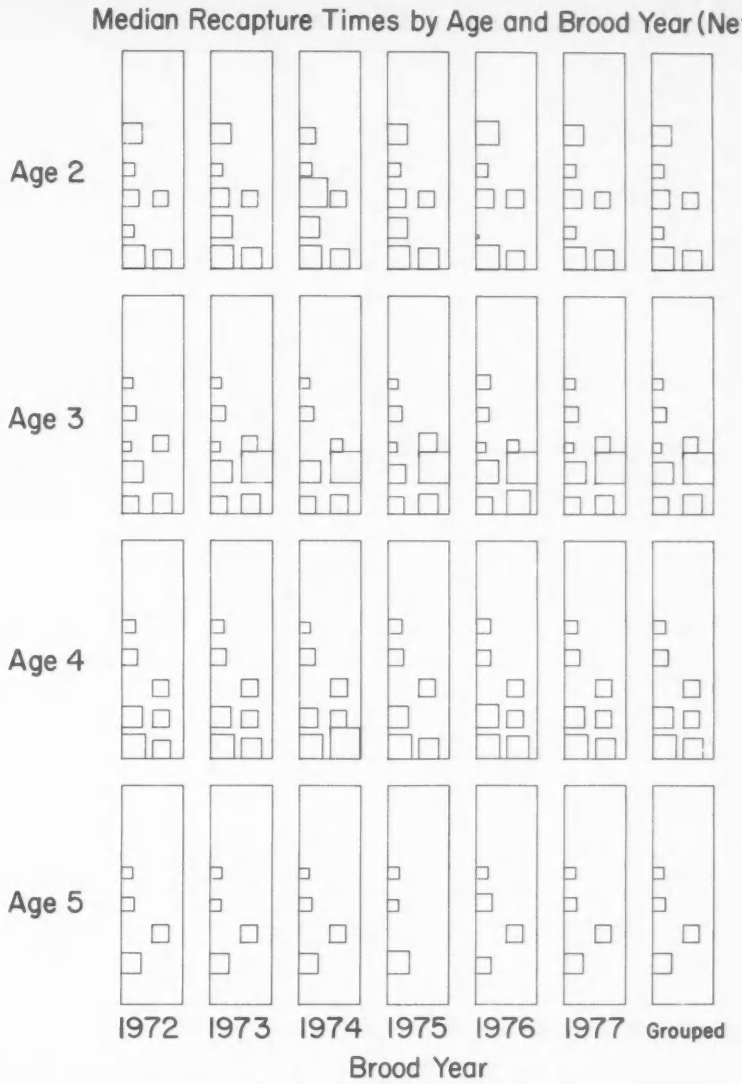

FIG. 3. Mosaics for combinations of brood years and ages using the median recapture times for the net fishery as the response variable. The mosaics on the extreme right are calculated by grouping the data for the brood years 1972–77 before calculating the median recapture dates.

less. The smile ranges up to sample sizes of approximately 1000. The fish are plotted in the same array as the one used in the mosaics for ages 2–5.

In this data set only the average lengths and sample sizes were available. Other morphometric measurements could also be represented in these drawings; for example, the depth of the fish in the drawing could be used to represent average weights, the width of the caudal fin could represent the variance of lengths, the width of the peduncle could represent the variance of weights, and a pectoral fin could be varied in location to represent the skewness of a distribution. In the faces of Chernoff (1973) and Flury and Riedwyl (1981) the data analyst must decide which variables to assign to which facial features, and different assignments can lead to different interpretations of the graphics (Chernoff and Rizvi 1975). With these fish the decision is easier, since there is a clear correspondence between the graphical symbol and the item being studied.

Interpreting the Mosaics and Fish Drawings

The following discussion is an attempt to interpret the graphs for possible biological meaning, based on the five questions posed earlier. The interpretation of a graph is to some extent a subjective matter, which is an advantage in that it promotes creativity but it also complicates consensus. The more interpretations, the more directions for future research on

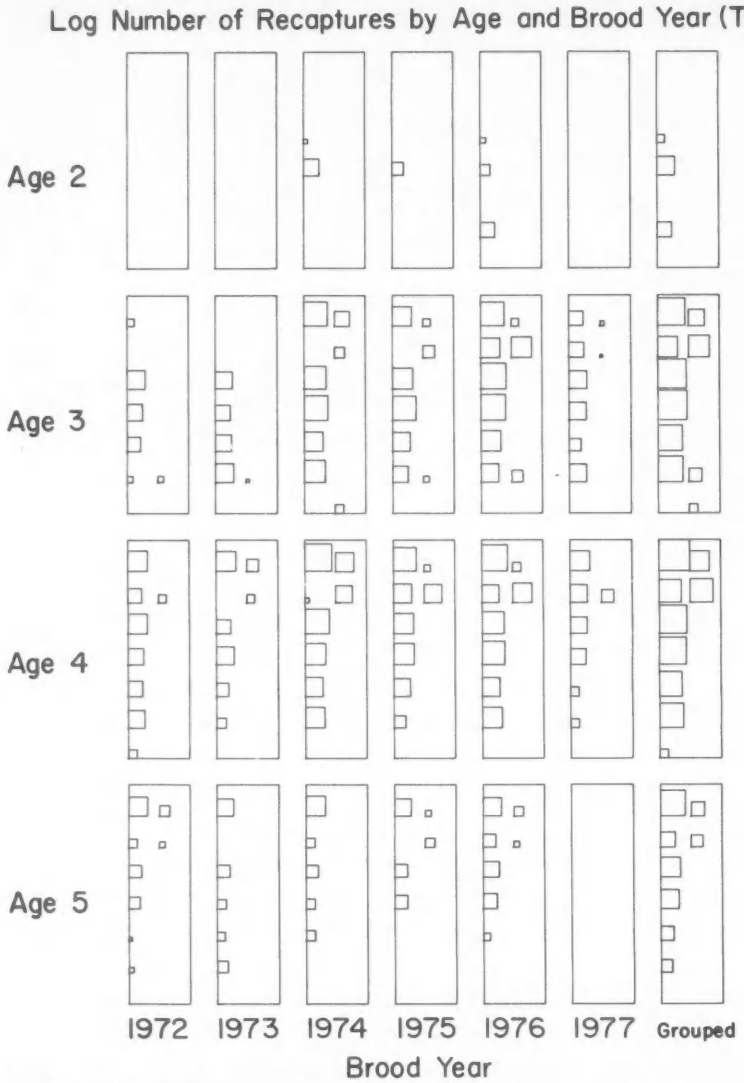

FIG. 4. Mosaics for combinations of brood years and ages using the logarithm of the number of recaptures for the troll fishery as the response variable. The mosaics on the extreme right are calculated by grouping the data for the brood years 1972–77 before calculating the logarithms.

salmon migration. The main point of the discussion is to demonstrate the use of the graphs as a data analysis tool for generating hypotheses about migration, not to decide which hypothesis is the most plausible.

Question 1

With these graphs the first question is answered quickly. Comparing the mosaics for the troll and net data (Fig. 2 vs. Fig. 3 and Fig. 4 vs. Fig. 5), one immediately notes that the data appear much more "random" for the net data. There are less, if any, patterns. This judgement can be made without even knowing what the graphs represent. What information can be deduced from such haphazard mosaics in the case of the net data? The difference in quality of the two pairs of graphs may be due to the fact that the troll fishery is directed at chinook salmon, despite some restrictions on where trollers can fish. In the net fishery, chinook are incidental to the catch, in general.

Question 2

As was noted earlier, question 2 is not an overall level question and is less amenable to new hypotheses. It is worth examining, though, if for no other reason than to summarize some of the patterns observed. There are four major observations. First, it can be seen that there are no age 2 Robertson Creek chinook caught in Alaska. The minimum size limit for

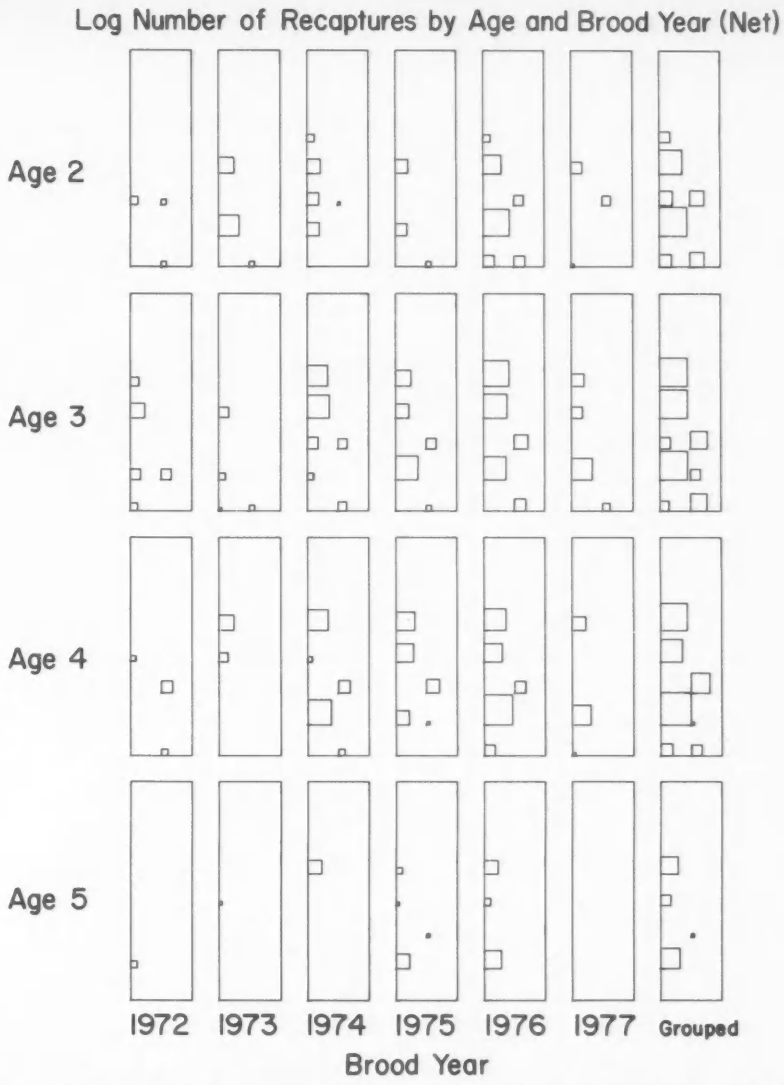

FIG. 5. Mosaics for combinations of brood years and ages using the logarithm of the number of recaptures for the net fishery as the response variable. The mosaics on the extreme right are calculated by grouping the data for the brood years 1972–77 before calculating the logarithms.

chinook in Alaskan waters is greater than the British Columbia limit, and this might explain the lack of catches reported; the other possible explanation is that the age 2 fish do not occur so far north. Second, in the net fishery, there were never any fish caught in Alaska. Third, the 1973 brood year seems to have done particularly badly in all age classes in the net fishery. Finally, recaptures of salmon in the waters south of Robertson Creek by the troll fishery are rare, occurring only in Washington–Oregon with age 4 fish of the 1972 brood year and age 3 fish of the 1974 brood year in Juan de Fuca Strait.

Question 3

Two consistent patterns relating to the direction of movement emerge in the troll data (Fig. 2). They are clearest in the grouped data. Along the left-hand sides of the arrays the squares increase in size from the top to the bottom of the array. This occurs in varying degrees for ages 3, 4, and 5. The second pattern is the small square at South Outside Alaska surrounded by bigger squares for the other Alaskan regions. There are no similar patterns for the net data (Fig. 3) although there is some consistency from year to year. The numbers of recaptures, though (Fig. 5), are highly variable. Recapture dates are often reported when only a small number of fish are caught. It is therefore difficult to infer much about migration from the net data.

These patterns are more difficult to recognize in the yearly data (Fig. 2). There is a large variability in the sizes of the squares from one year to the next for a given age. In part, the

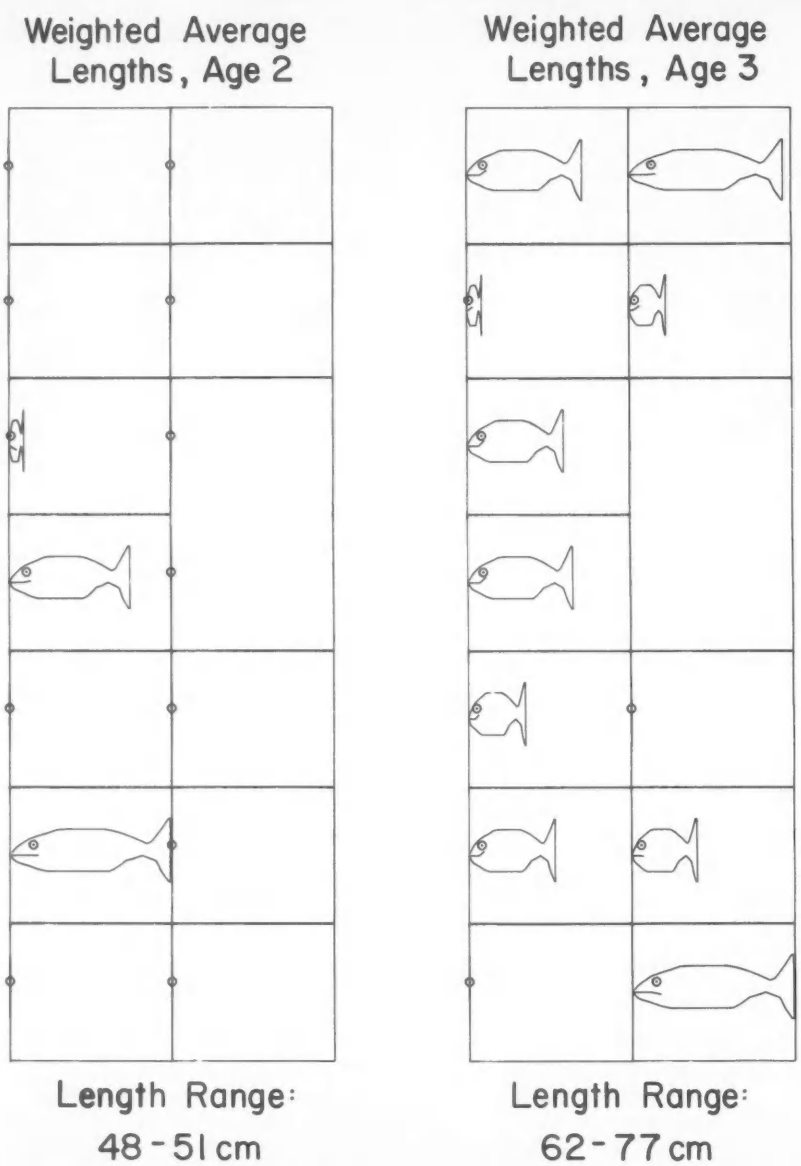

FIG. 6. The lengths of the fish drawings are proportional to the weighted average length of all age 2 (left) or age 3 (right) fish recaptured in a given commercial catch region by the troll fishery for the brood years 1972–77. The smiles are proportional to the logarithms of the sample sizes. Straight faces and frowns correspond to less than 25 fish, while smiles represent sample sizes of up to 1000 fish. The smiles can be compared with the squares in the grouped mosaics in Fig. 4, as they are calculated from the same number. The lengths of the fish drawings are scaled for each age; this means that drawings between ages cannot be directly compared.

variability might be attributed to differences in the number of recaptures. For example, the first pattern appears to hold to some degree for age 3 fish at least in the brood years 1972, 1976, and 1977. In the 1976 brood year the median recapture date in Georgia Strait appears earlier than Southwest Vancouver Island, which is contrary to the pattern. Looking at the number of recaptures for this same location (Fig. 4), we see that relatively few fish were caught. The square is approximately just less than half its full possible dimensions, meaning the number of recaptures was less than 20. The variability in the graphs from one year to the next may also be attributable to the "brood year effect" discussed in Green and Macdonald (1987).

One possible hypothesis that would explain these patterns

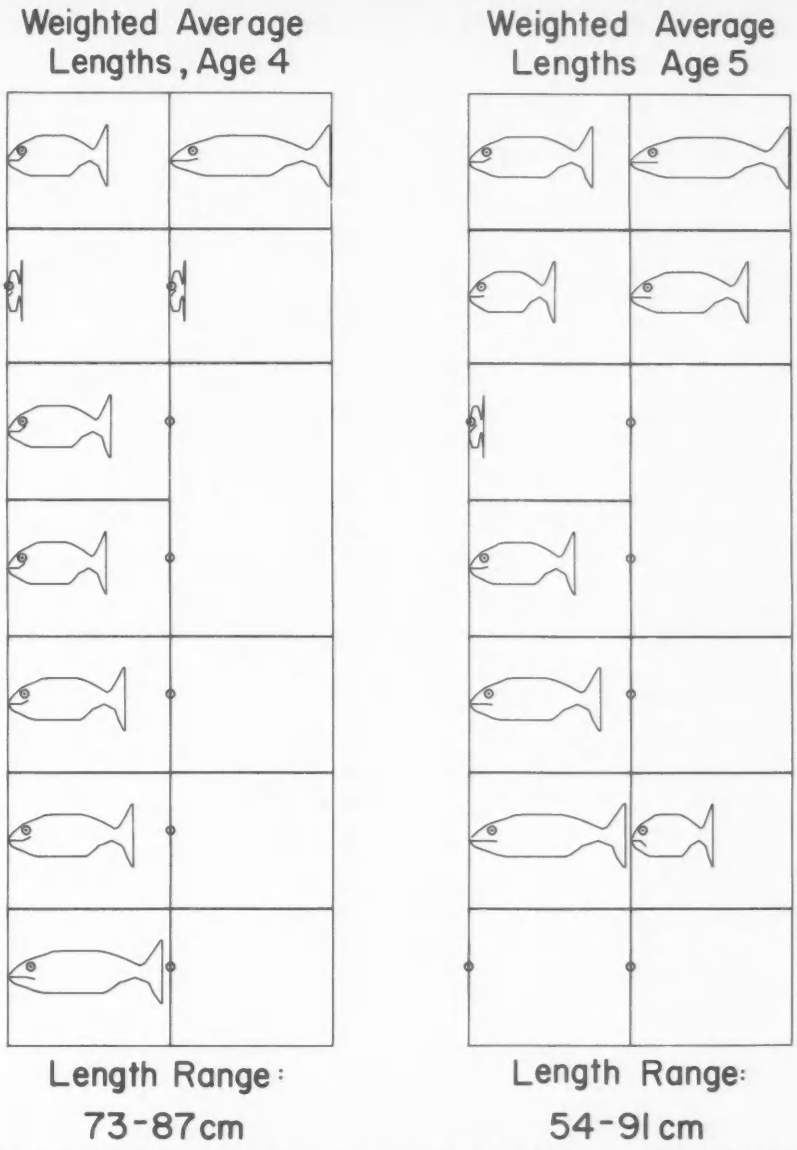

FIG. 7. The lengths of the fish drawings are proportional to the weighted average length of all age 4 (left) or age 5 (right) fish recaptured in a given commercial catch region by the troll fishery for the brood years 1972–77.

would be that during the fishing season the age 3, 4, and 5 salmon begin their migration at South Outside Alaska. Some swim south, and other migrate into the other Alaskan regions. This hypothesis rests on the assumption that the chinook do not migrate by linear radial scattering and that the patterns are not due to artifacts of fishing effort. The two patterns observed in the grouped data may be underlying the observations in the yearly data, but it is impossible to tell.

Question 4

For the troll fishery, there is a trend towards decreasing recaptures in the southern regions. This is especially apparent for age 4 fish and in the grouped data for ages 3–5. For the net data there are no obvious patterns. There are three possible hypotheses that could explain the trends in numbers of fish recaptured by the troll fishery. The trend could be due to either decreasing fishing effort, decreasing numbers of fish available to be caught, or a decreasing tendency on the part of the fish to take the troll gear as they migrate towards their natal stream in the south. Even if fishing effort data were available, it would be impossible to distinguish between the latter two alternatives.

Question 5

Some of the same trends seen in the mosaics are seen in the fish drawings (Fig. 6 and 7). The smallest fish are caught in South Outside Alaska, northern British Columbia, or South Inside Alaska, which are also, generally speaking, the areas in which the fish are caught earliest (Fig. 2). Except for age 3, the fish become progressively larger towards the southern regions. For all ages for which there are data the fish caught in the northern Alaskan regions are relatively large.

An hypothesis that would explain this combination of earlier recapture times and large size would be that the fish caught in Alaska are growing at a faster rate than the fish migrating southwards. If this was due to a lower food intake of the fish migrating southwards, the decreasing number of recaptures seen in the southern regions in the troll data (Fig. 3) could, then, also be explained, since fish that were eating less would have less of a tendency to attack a lure. The net fishery does not depend on the fish attacking the lures, which could partially explain the absence of patterns.

In summary, the major observations and hypotheses generated by this graphical analysis are (1) the net data are more haphazard as compared with the troll data, possibly due to the fact that the net fishery is incidental and the troll fishery directed towards chinook; (2) the earliest median recapture dates are in the South Alaska statistical area with increasing medians moving southwards: the salmon could be migrating outwards from the South Outside Alaska statistical region, some going north into other Alaskan regions and some going south; (3) the salmon are caught by troll gear in decreasing numbers as they move southwards, either because the salmon are eating less or because there is less fishing effort applied; and (4) the fish caught by troll gear south of Alaska appear to be growing at a slower rate than those caught in Alaska.

Discussion

These mosaics are useful tools for studying the movement and distribution of fish caught by commercial fishing vessels and for generating hypotheses about their migration behaviour. By simplifying the geographical regions as has been done here, repeating them for the desired combination of ages and years (if possible), and plotting median recapture (or catch) dates and numbers of recaptures as squares in the geographical regions, hypotheses and questions can be generated about fish migration. This is an indirect way of studying migration using commercial data; it is not necessary to carry out specific migration experiments. In this analysis the situation was relatively simple in that we were dealing with identifiable stocks of fish from the Robertson Creek hatchery. This technique would be very appropriate for other stocks of fish tagged with coded-wire tags or some other mark, but could also be attempted for commercial catches when it was thought that the fish were coming more or less from the same stock or at least migrating in the same general way. The fish drawings are useful tools for studying the morphometrics of the fish as they migrate.

Acknowledgments

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References

Bertin, J. 1967. Sémiologie graphique. Mouton, Paris, and The Hague. 431 p. (In French)

1981. Graphics and graphic information-processing. de Gruyter, Berlin and New York. 273 p. (Transl. from French by W. J. Berg and P. Scott)

Chambers, J. M., W. S. Cleveland, B. Kleiner, and P. A. Tukey. 1983. Graphical methods for data analysis. Duxbury, Boston, MA. 395 p.

Chernoff, H. 1973. The use of faces to represent points in k-dimensional space graphically. J. Am. Stat. Assoc. 68: 361–368.

Chernoff, H., and M. Rizvi. 1975. Effect on classification error of random permutations of features in representing multivariate data by faces. J. Am. Stat. Assoc. 70: 548–554.

Dondis, D. A. 1973. A primer of visual literacy. MIT Press, Cambridge, MA. 194 p.

Flury, B., and H. Riedwyl. 1981. Graphical representation of multivariate data by means of asymetrical faces. J. Am. Stat. Assoc. 76: 757–767.

Green, P. E. J., and P. D. M. Macdonald. 1987. Analysis of mark–recapture data from hatchery-raised salmon using log-linear models. Can. J. Fish. Aquat. Sci. 44: 316–326.

Harden Jones, F. R. 1968. Fish migration. Arnold, London. 325 p.

Hartigan, J. A., and B. Kleiner. 1984. A mosaic of television ratings. Am. Stat. 38(1): 32–35.

Jacob, R. J. K. 1981. Comment. J. Am. Stat. Assoc. 76: 270–271.

Nicholson, M. D., and J. A. Pope. 1977. The estimation of mortality from capture–recapture experiments, p. 77–85. *In* J. H. Steel [ed.] Fisheries mathematics. Academic Press, London.

Quinn, T. P., and C. Groot. 1984. Pacific salmon (*Onchorynchus*) migrations: orientation versus random movement. Can. J. Fish. Aquat. Sci. 41: 1319–1324.

Royce, M. P., L. S. Smith, and A. C. Hartt. 1968. Models of oceanic migrations of Pacific salmon and comments on guidance mechanisms. U.S. Fish Wildl. Serv. Fish. Bull. 66(3): 441–462.

Saila, S. B., and R. A. Shappy. 1963. Random movement and orientation in salmon migration. J. Cons. Perm. Int. Explor. Mer 28: 53–166.

Tufte, E. R. 1983. The visual display of quantitative information. Graphic Press, Cheshire, CT.

Seminatural Rearing of Atlantic Salmon (*Salmo salar*) in Newfoundland

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Pepper, V. A., T. Nicholls, and N. P. Oliver. 1987. Seminatural rearing of Atlantic salmon (*Salmo salar*) in Newfoundland. Can. J. Fish. Aquat. Sci. 44: 337–347.

Atlantic salmon fry (*Salmo salar*) obtained from an artificial spawning channel and a deep-substrate incubator, were reared in mesh "troughs" in an artificial rearing channel and in floating lake cages. Fry placed in the lake cages were able to complete their first feeding phase on a diet of natural lake zooplankton but growth performance was improved when artifical diets were used to supplement natural food. Parr fed selectively on *Daphnia catawba* and mature *Epischura lacustris*. Parr reared in the mesh troughs were hand-fed a commercial diet. The 90-d average release weight ranged from 1.8 to 3.1 g for parr from the mesh troughs and from 0.9 to 3.1 g for parr from the lake cages. Growth of parr in these experiments resulted in an average weight advantage of approximately 2.3–4.5 times over parr captured from natural riverine habitat at the end of the experiment. Overall swim-up fry to fall-fingerling survival from these experiments was 52% in 1983 and 76% in 1984. Survival and growth varied inversely with density in the mesh trough experiments.

Des alevins de saumon de l'Atlantique (*Salmo salar*), provenant de frayères artificielles et d'incubateurs à substrats profonds ont été élevés dans des « auges » en treillis mouillées dans des bassins d'alevinage artificiels et des cages flottantes en milieu lacustre. Les alevins placés en cage ont pu terminer leur première phase d'alimentation à l'aide d'un régime de zooplancton lacustre naturel; cependant, le rendement de croissance a été amélioré par l'apport de suppléments aux aliments naturels. Les tacons se sont nourris de façon sélective de *Daphnia catawba* et d'individus matures de *Epischura lacustris*. Ceux élevés dans les auges en treillis ont été nourris manuellement d'aliments achetés dans le commerce. Le poids moyen au lâcher après 90 j variait de 1,8 à 3,1 g chez les tacons élevés dans les auges en treillis et de 0,9 à 3,1 g chez ceux élevés dans des cages en milieu lacustre. La croissance des tacons observée au cours de ces expériences révèle un avantage pour ce qui est du poids moyen qui est environ de 2,3 à 4,5 fois plus élevé que celui de tacons capturés dans un habitat fluviatile naturel à la fin de l'expérience. La survie globale depuis le stade d'alevin nageant jusqu'au tacon d'automne, obtenue au cours de ces expériences, s'élevait à 52 % en 1983 et à 76 % en 1984. La survie et la croissance ont varié en raison inverse de la densité au cours des expériences dans les auges en treillis.

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Historically, Atlantic salmon (*Salmo salar*) enhancement in Newfoundland has been based on stream remedial and stream clearance activities, adult spawner transfers, and swim-up fry distribution to stream nursery areas (Farwell and Porter 1976). By the late 1960s, most of Newfoundland's enhancement activity was based on distribution of swim-up fry, from a controlled flow spawning channel, to suitable stream habitat (Pratt 1968; Sturge 1968; Pratt et al. 1974). Subsequent pursuit of this approach has proven, at least for the freshwater habitats of this province, that unfed fry distributions have considerable merit (Farwell and Porter 1976; O'Connell et al. 1983). Our more recent experiments (Pepper et al. 1985) have encouraged continuation and expansion of fry distribution to shallow-water lacustrine nursery areas in Newfoundland. While further refinement of lacustrine release of swim-up fry may secure a potential for natural salmon production, evidence that fry-to-smolt survival in lacustrine habitat decreases in the presence of consecutive year-classes (Pepper et al. 1985) has led to interest in investigating fall-fingerling salmon as an alternative to fry for release.

In the absence of proven methodologies for rearing fall-fingerling Altantic salmon in relatively uncontrolled semi-natural environments, approaches taken in the present research have been largely exploratory. We describe seminatural rearing experiments in Newfoundland in 1983 and 1984. Our results are intended to provide a base from which to structure more rigorous experimental designs for development of effective seminatural salmon culture practices.

Materials and Methods

Seminatural rearing experiments were conducted at, or in the environs of, the Indian Brook research station (49°26′N, 56°29′W). Atlantic salmon of grilse × grilse anadromous parents were obtained from a deep-substrate incubator and from the Indian Brook spawning channel, the upper 30 m of which has been modified for fry rearing (Fig. 1). This rearing area is composed of two 15-m pools at the upper end of the channel.

Fry from the spawning channel were placed in two types of seminatural rearing enclosures: (1) mesh troughs secured within the rearing channel and (2) floating lake cages. Spawner density, sex ratio, flow rates, and other operational variables relating to egg deposition and incubation in the spawning channel were controlled as per Pratt (1968) and Davis and Farwell (1975).

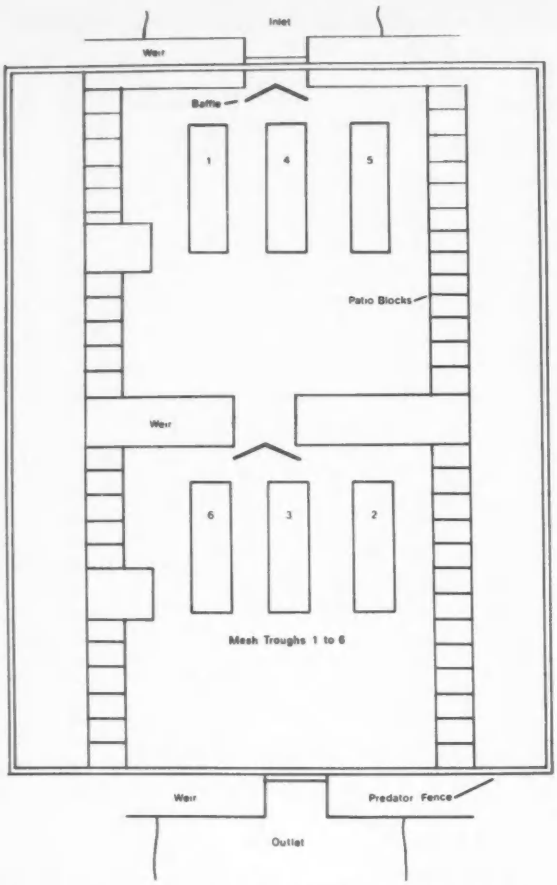

FIG. 1. Seminatural rearing channel pools and mesh trough placement.

Rearing Channel

The bottom of the rearing pools is composed of gravel and rubble (4–8 cm). The banks are stabilized by concrete patio blocks laid side by side at an approximate 30° angle. A predator control fence of 16-gauge, 1.3-cm hardware cloth surrounds the pools to exclude mink (*Mustela vision*) and other small predators. The rearing enclosure is covered by 10-cm gill netting to exclude avian predators (i.e. mergansers (*Mergus merganser*) and kingfishers (*Megaceryle alcyon*)).

Water enters the pool through a weir with a 1.5-m-wide opening. Removable 6-mm-mesh screens were installed at the entrance and exit of each weir to exclude debris and predators from the rearing area. Plywood baffles with 6-cm holes were installed at the upper end of each of the two rearing enclosures below each weir to provide a more uniform water flow throughout most of the area of the pools. A surface water velocity of approximately 6–10 cm/s was maintained throughout the rearing period. Stoplogs were used at the lower pool exit to control water levels in both pools. Water flow could be controlled by a valve located at the entrance to the rearing channel.

Fry were collected from Wolf traps located at the lower end of the spawning channel, counted (California volumetric estimation, Leitritz and Lewis 1976), and placed in mesh troughs in the rearing pools. Mesh troughs consisted of a plywood bottom (1.22 × 4.88 m) painted with gray antibacterial paint and sides of 0.16-cm knotless nylon mesh, reinforced at the corners and supported by corner posts (Fig. 2a). Mean water depth in the mesh troughs was regulated to 20 cm for the first feeding period for all units. This was adjusted to 30 cm when all fry were feeding well and distributed throughout the water column. The number of fry placed in each mesh trough was regulated according to desired density.

Fry density at the beginning of the experiments in 1983 was examined at three levels (i.e. wet weight = 5.6, 4.1, and 3.2 g/1000 cm^3); each density was replicated once over the six mesh trough units. Mesh troughs were filled in pairs so that each duplicate of a given density level was examined over the same time interval.

No attempt was made to feed fry during the initial 2–3 d following their allocation to the mesh troughs. Fry mortality during this interval was attributed to handling stress as a result of collection and enumeration. All dead fry were removed from the mesh troughs daily during this interval and were not replaced. In consideration of the physiological consequences of handling stress (Black and Barrett 1957; Mazeaud et al. 1977; Wedemeyer et al. 1980), fry were immersed for 20 min in a 2% static NaCl bath whenever daily mortality increased over more than 3 consecutive days. Two salt treatments were administered in 1983 by transferring parr in batches from each of the mesh troughs to a 1.5-m-diameter circular tank that was set up within the rearing pool. Fry from each mesh trough were transferred back to their rearing unit before the next lot was processed.

Mesh trough experiments in 1984 were based on lower fry densities (i.e. wet weight = 2.8, 1.4, and 0.8 g/1000 cm^3). Only four mesh troughs were used. Rather than awaiting early rearing mortality before implementing salt treatment, iodized salt licks (4 kg/d) were introduced to the rearing channel water intake.

During the intervals in which the rate of fry mortality was of concern in 1983, samples of dead and of moribund fry were placed on ice and shipped immediately to the Fish Health Laboratory (Department of Fisheries and Oceans, 1707 Lower Water Street, Halifax, N.S. B3J 2S7) where they were examined for bacterial and viral agents as per Schedule II of the Canadian Fish Health Protection Regulations (Government of Canada 1984).

Small quantities of food were offered to the parr by hand when about 50% were observed swimming in the water column. Thereafter, parr were fed to excess at hourly intervals (09:00–17:00). Swim-up fry initially were fed a mixture of 75% Biodet No. 2 (Lemm and Hendrix 1981) and 25% dry Silver Cup (Murray Elevators, Murray, UT) starter. They gradually were weaned to a 100% Silver Cup dry diet after 39 d. Food particle size and mix ratio depended on the mean size of the fish, following Silver Cup feeding guidelines.

All mesh troughs were cleaned thoroughly once per day with a soft bristle brush, usually in the morning while water temperature was lower. All mortalities were removed and counted. The trough bottoms and sides were scrubbed to remove faeces, food, and algal material.

Depth of water in the net pens was increased to reduce possible crowding stress and oxygen depletion during periods of extremely high water temperatures. Water flow also was increased slightly at these times. Water temperatures were

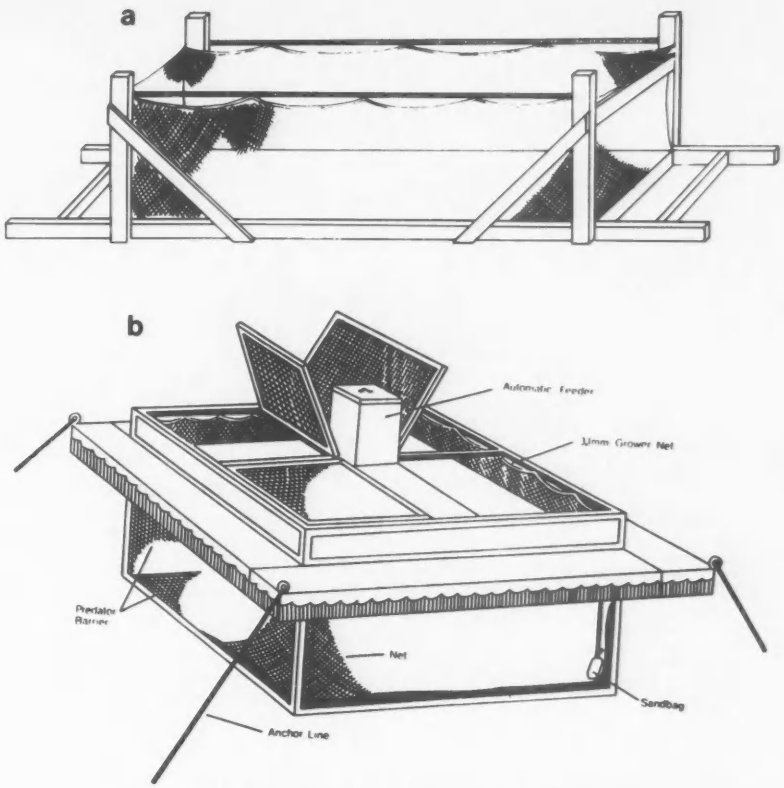

FIG. 2. Seminatural rearing enclosures for Atlantic salmon.

taken hourly by hand thermometer during the working day. A recording thermography provided a continuous temperature record. Oxygen determinations were done only occasionally. Oxygen concentrations were obtained with a YSI electronic O_2 meter, typically only on very warm days (water temperature >18°C). These readings were taken both before and after feeding.

Lake Cages

The lake cage (Fig. 2b), described by Slaney and Harrower (1981), was adapted for our experiments. Our cages measure 3.6 × 3.6 × 1.8 m deep and are made of 1.6-mm delta-type knotless nylon mesh treated with an antifouling preservative (Plastiseal).

Lake cage experiments in 1983 were designed to investigate and evaluate feeding strategies. One shallow net (3.6 × 3.6 × 1.0 m, 1.6-mm mesh) was installed in early June 1983 at which time 5800 swim-up fry were transferred to the cage from the spawning channel. The fry in this unit were virtually unattended for the first 40 d. The only food source during this interval was the natural lacustrine zooplankton population. Two more cages were installed after the initial 40-d interval in 1983 at which time the 40-d experiment was terminated. All three cages then were fitted with 1.8-m-deep nets (3.1-mm mesh) and fry from the first cage were distributed equally among the three units. Concurrently, fed fry were transferred by truck from the Indian Brook rearing channel (mesh troughs 2, 3, and 6) and also were distributed evenly to the three lake cages. A different feeding level was applied to each lake cage. Cage 1 parr were fed excess rations at 12 food portions per day at hourly intervals during the daylight hours (8–10% body weight/d). Cage 2 received four portions per day, one portion every 2 h (2–3% daily). Food was dispensed in cages 1 and 2 by Sweeney turkey feeders (model DF1-12V dc). Progression in size of artificial food granules followed the schedule applied in the rearing channel. Cage 3 received no artificial food. Parr in this cage relied solely on natural zooplankton as the main diet.

Four vertical plankton tows were taken from July to September both from within the cages and at a point 5 m from the cage platform. All tows were taken with an 80-μm plankton net (30-cm throat, Wisconsin) covered with 1.6-mm-mesh minnow seine to prevent parr from entering the zooplankton bottle. These tows sampled the upper 1.8 m of the water column (one vertical tow through the same depth as the cages). Zooplankton samples were preserved immediately in 10% formalin and identified 5 mo later. Samples were graded into size categories with nested sieves (2, 1, 0.5, and 0.25 mm). The resulting segregated size categories were examined, component zooplankton identified to species, and the individuals counted. All samples were counted in their entirety on a grid background.

Weekly fry samples were taken throughout the 1983 experiments. A sample of 20 fry was taken from each cage and preserved (10% formalin) on site for later stomach contents

analyses. Live samples of 50 fish were weighed and measured individually once each week and subsequently returned to the nets. These data were used to monitor growth rates.

Parr stomach contents were examined with a dissecting microscope. A subjective estimate was made of the degree of fullness of each stomach (point method of Kislalioglu and Gibson 1977). The proportion of artifical food versus zooplankton was estimated for those fish that were fed a commercial diet. All identifiable zooplankton were enumerated and arranged in order of decreasing proportion. In the case of fragments, numbers of animals were estimated by counting heads (for cladocerans) or bodies (for copepods).

Cages were cleaned with a long-handled brush every 2–3 d during the first 40-d experiment. A gas-powered water pump with a high-pressure nozzle was used to clean algal and detrital material from the net mesh for the remainder of these experiments. While nets were being cleaned, fry were confined in one half of the net so the other half of the net could be drawn to the surface and subjected to the high-pressure spray. All mortalities were removed and counted.

Methods used for lake cages in 1984 were basically the same as for 1983. Emphasis was placed on more frequent cleaning of the units (daily) and insuring that fry were receiving measured amounts of food. Three different quantities of fry were used in 1984 (5000, 10 000, and 15 000). Artifical food was used to supplement fry diets throughout 1984 and daily food allotments were calculated in the same manner as for the rearing channel fish (i.e. a maximum of 12% body weight/d). Automatic feeders were set to feed 12 times per day during the daylight hours.

Experiments were terminated in late September in 1983 and early October in 1984 at which time fall-fingerlings were enumerated and sampled to determine mean length and weight. All parr then were released into natural freshwater habitats. Samples of wild fall-fingerlings were obtained in 1984 by electrofishing in the main stem of Indian Brook, adjacent to the rearing channel. These samples were obtained, concurrent with the final rearing experiment samples, to allow growth comparison between wild parr and those from our seminatural rearing experiments.

Data Analysis

Data analyses in 1983 were limited to simple evaluations of growth (based on mean length and weight per sample period) and mortality (percent per day). Daily instantaneous growth was calculated as

$$\frac{\log_e \text{Variable}_{t+1} - \log_e \text{Variable}_t \times 100}{t}$$

where Variable = mean total length or mean wet weight (grams) and t = time (days) between sampling periods.

Data analyses for the 1984 experiments were more rigorous. Analysis of growth performance in the six rearing units (three mesh troughs plus three lake cages) was pursued by covariance techniques. Separate regressions were undertaken for weight with time and length with time. Weight–length analyses also were pursued by this method.

Growth in total length (total length on days) and in weight (live weight on days) was examined by standard least squares regression. Particular attention was paid to the behavior of error variances in these regressions. Regressions of transformed data (weight and length) and weighted least squares regression (Draper and Smith 1981) also were evaluated. Comparison of regression slopes was by standard analysis of covariance (Zar 1974). The Statistical Analysis System (SAS) was used to evaluate growth performance in the various units.

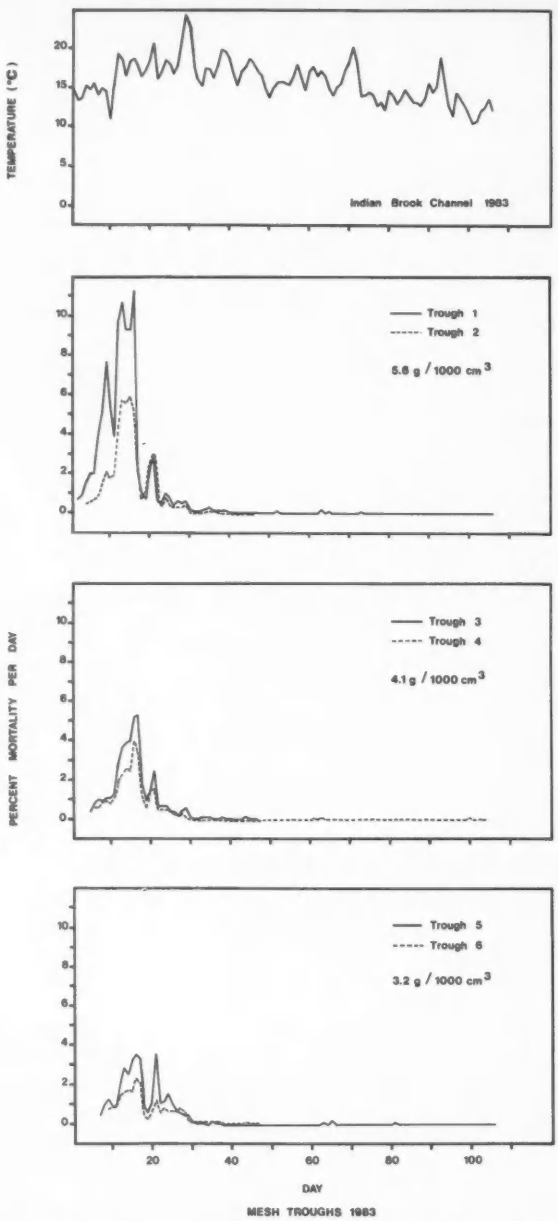

FIG. 3. Temperature and mortality patterns throughout Atlantic salmon rearing experiments in 1983.

Results

Fry emigrated from the spawning channel from June 5 to June 16 in 1983. Thus, rearing time for the last rearing unit

TABLE 1. Water chemistry for Indian Brook study area (units in mg/L).

Chemical parameter	Indian Brook levels		Hatchery standards[a]		
	Min.	Max.	Min.	Max.	Optimum
Alkalinity (as $CaCO_3$)	1.1	18.8	10	400	120–400
Hardness (as $CaCO_3$)	3.1	20.2	10	400	120–400
Nitrate	<0.002	0.041	0	3	
Orthophosphate	0.006	0.022			
Total phosphate	0.019	0.22	0.01	3	
Calcium	0.50	4.70	4	160	<52
Magnesium	0.078	2.80			
Manganese	<0.01	0.05	0	0.01	
Iron	0.05	0.34	0	0.15	
Zinc	<0.01	0.040	0	0.05	
Sulfate	0.820	2.00			
Chloride	1.200	3.40			
Sodium	0.520	2.80			
Potassium	0.090	0.54			
Total dissolved solids	11.0	61.0			
pH	6.12	6.84	6.5	8.5	

[a]From Piper et al. (1982).

started 10 d after the first. Mortality through the first 7–8 d of the experiment was low regardless of the starting density. Mortality increased greatly for all mesh troughs during the second and third weeks (Fig. 3). No bacterial or viral pathogens were identified; oxygen levels were near saturation in both the intake and outlet areas of the channel, both before and after feeding; and pH ranged from 6.12 to 6.84. In the absence of any known cause for this mortality, we speculated that fry were suffering from mineral deficiencies (water chemistry data, Table 1) that were causing osmoregulatory stress. Salt baths, administered in late June, were followed by reduced mortality that began to rise once again 2 d later. Mortality dropped to minimal levels after administering the second salt bath. The rate of mortality in the lake cages remained relatively stable and no salt baths were required. Survival of parr in the lake cage during this period was 67%, while survival rates in the mesh troughs ranged from 26 to 79%. Overall parr survival (mesh troughs) during the first 40 d was 61.0%.

Survival of the three density groups in the mesh troughs in 1983 varied through the first 40-d rearing period. Survival in the "high"-density group was 49% (mesh troughs 1 and 2 combined). The "medium"-density group (mesh troughs 3 and 4) survival was 69%, while "low"-density survival was 73% (mesh troughs 5 and 6). No further mortality problems were experienced after the initial 40-d rearing period. Survival of parr in the three lake cages, from day 41 to the end of the 1983 experiment (i.e. after transfer of channel-reared parr), ranged from 94 to 97%. Survival of mesh trough parr in the remaining units, from day 41 to the end of the experiment, was 99%. Overall survival for all units through the duration of the 1983 experiments was 52%.

Fry emigration from the spawning channel in 1984 took place between June 2 and July 4. Emigration from the deep-substrate incubator occurred from May 28 to July 10. Early rearing mortality in 1984 was less than in 1983 (Fig. 4). Salt solution baths were necessary in only two of the units and once again proved effective. Survival over the first 40 d of the rearing channel experiments ranged from 79 to 92% (mean = 83.8%). Overall survival in the lake cages for the first 40 d ranged from 83 to 98% (mean = 88.9%). Once again, salt treatments were not required for the lake cages. Overall survival for mesh troughs ranged from 64 to 85% for the 1984 experiment (mean = 76.8%). Lake cage parr survival for this period ranged from 66 to 88% (mean = 75.3%).

TABLE 2. Zooplankton species from lake cage rearing experiments with Atlantic salmon parr. Numbers represent pooled total counts from four vertical plankton tows.

Zooplankton	Pond	Natural food cage	Artificial food cage 3%/d	Artificial food cage 9%/d
Cladocerans				
Daphnia catawba	24	1	2	2
Holopedium gibberum	2	0	0	0
Diaphanosoma birgei	15	2	1	2
Bosima longirostris	3	18	27	8
Copepods				
Epishura lacustris	7	1	1	13
Diaptomus minutus	39	74	89	25
D. spatulocrenatus	9	2	0	1
Cyclops	15	98	41	0

TABLE 3. Lake cage parr stomach contents. Pooled zooplankton counts from 57 parr stomaches/feeding category.

Prey item	Natural food cage	Artificial food cage 3%/d	Artificial food cage 9%/d
Daphnia catawba	734	419	2769
Episura lacustris	113	28	182
Bosmina longirostris	524	95	148
Holopedium gibberum	11	2	8
Sida crystallina	6	1	15
Diaphanosoma birgei	20	0	11

During daylight hours, parr in the mesh trough experiments were distributed throughout the 30-cm water column and exhibited some tendency to crowd to the front of the units. At night, parr settled to the bottom of the troughs and were distributed evenly over the entire trough bottom.

The initial response of fry when stocked in lake cages was to settle to the bottom and remain relatively inactive for about 30 min. Thereafter, they began to distribute themselves throughout the water column although they appeared to exhibit an affinity for the sides of the cage. They often were observed to rest in creases in the mesh at angles of less than 30° off vertical. This apparent attraction to the sides of the net was more pronounced (subjective interpretation) during the second phase of the lake cage experiments when parr densities were higher. All swimming movement was of an apparently calm, exploratory nature.

Large masses of zooplankton were evident within the lake cages throughout the rearing period (Table 2). Analysis of stomach contents confirmed the observation that parr were feeding on zooplankton (Table 3). Feeding on zooplankton within the cages was virtually continuous. Feeding activity increased to "frenzy" level when the automatic feeders were activated. It was apparent that caged parr were obtaining some diet supplement from natural food organisms due to the orange hue that developed on the fins and bodies of a large percentage

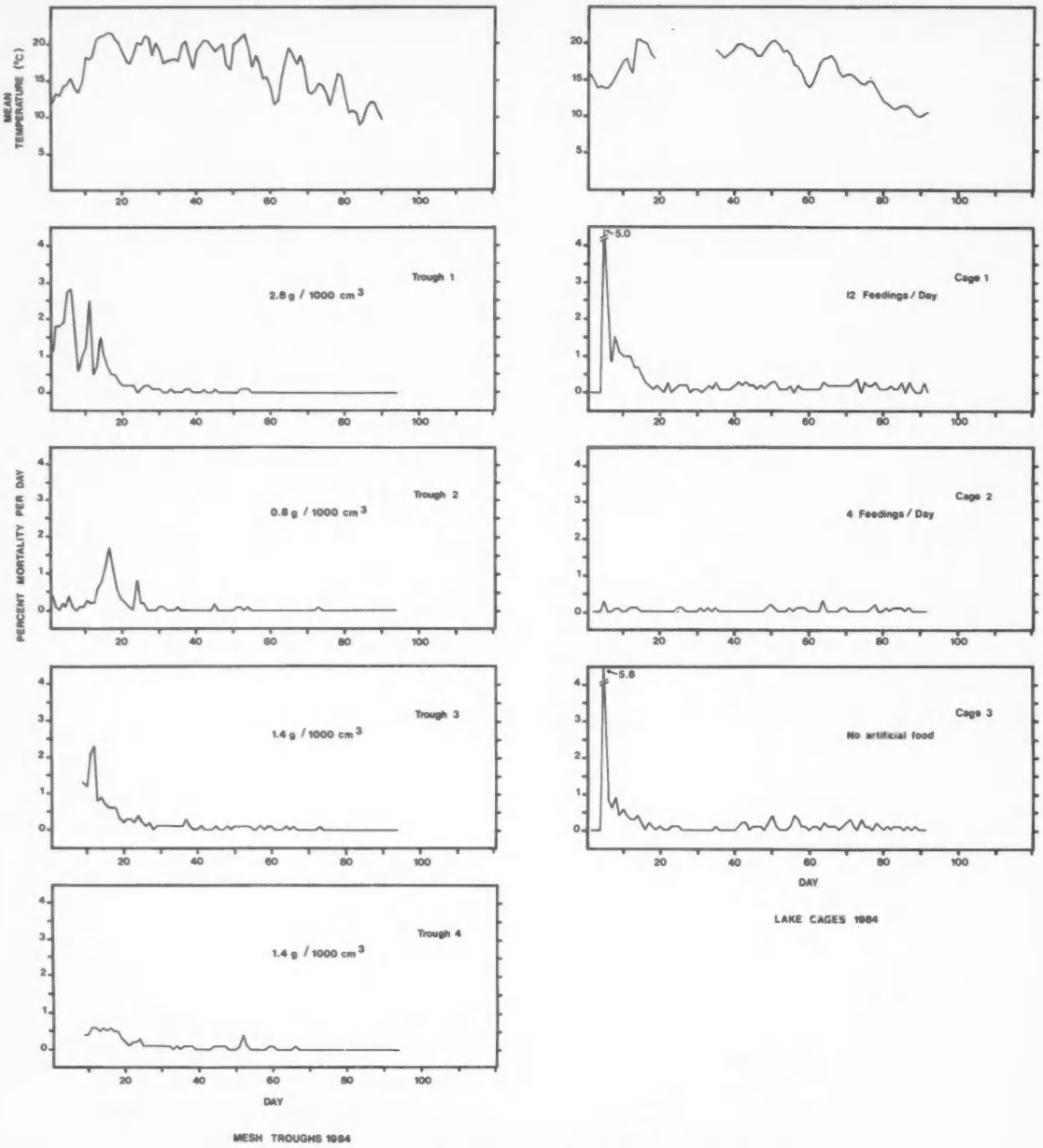

FIG. 4. Temperature and mortality patterns throughout rearing experiments in 1984.

of these fish. This coloration was in sharp contrast with the mesh trough specimens that retained a silvery green coloration throughout the experiment.

Although analysis of stomach contents was undertaken simply to confirm that parr were ingesting zooplankton, stomach contents also revealed the intensity of feeding in the respective cages. As expected, parr receiving the greatest amount of food had the fullest stomachs. Those that had access only to natural zooplankton had little in their stomachs.

Juvenile calanoids (mostly *Diaptomus minutus*) were the most plentiful of the zooplankton species found within the lake cages (Table 2). All zooplankton passed through the 1.0-mm sieve. Although *Daphnia catawba* was by far the most numerous species found in the stomach samples, it was not abundant among zooplankton samples. A further dichotomy between stomach contents and zooplankton samples was the prevalence of large mature specimens of *Epischura lacustris* in the stomachs. Zooplankton samples contained mostly imma-

TABLE 4. Growth function parameters (total length on day) for 1984 salmon parr rearing experiments.

Method	Unit	Density (g/1000 cm³)	Regression parameters				Regression slopes		
			Intercept	Slope	R^2	MSE	F	P	N
Mesh trough	1	2.8	23.894	0.421	0.88	2.288	9.77	0.001	600
	2	0.8	24.834	0.452	0.90	2.417			600
	3	1.4	25.956	0.392	0.86	2.225			580
Lake cage	1	Highest	26.159	0.294	0.61	2.889	9.48	0.001	580
	2	Intermediate	27.653	0.394	0.69	3.287			580
	3	Lowest	27.503	0.329	0.66	2.926			580

ture specimens. Another general pattern is that artificial food was present in the pyloric end of the stomach, while the cardiac end and alimentary tract contained zooplankton. Zooplankton of the same species often were clumped together in parr stomachs. Although not routine among stomach contents, *Bosmina longirostris* and *Diaphanosoma bergei* were found in some stomachs to the virtual exclusion of other species.

The degree of stomach filling was similar between parr of the two artificial food supplement cages and generally contained about twice the amount of material relative to parr stomachs from the natural feed cage. Cages receiving artificial food supplements had a much greater accumulation of detritus and algal fouling of the mesh. The frequency hydraulic cleaning was effective in limiting this fouling to a tolerable level.

Wild fall-fingerlings ($N = 59$) obtained from the main stem of Indian Brook at the same time that final samples were taken from the rearing experiments had a mean total length (TL) of 4.34 cm (standard deviation = 2.61) and mean wet weight of 0.7 g (standard deviation = 0.12). Final mean sizes in the seminatural rearing experiments ranged from 5.33 cm TL and 1.6 g wet weight to 6.76 cm and 3.1 g (Fig. 5). The best growth rate for these experiments was found in the low-density mesh trough in 1984. Instantaneous growth in this unit during the 92 d of the experiment averaged 3.09% body weight/d.

Simple linear regression of total length on days for six of the rearing units in 1984 indicated highly significant linear equations ($P < 0.0001$). Ranges for the unexplained error component of these regressions did not overlap (R^2 lake cages = 0.38–0.49; R^2 rearing channel = 0.83–0.86). Plots of the error variance versus fitted total length from the least squares regressions revealed a pronounced wedge-shaped pattern. An attempt to overcome these nonconsistent error variances, using a square root transformation as recommended by Draper and Smith (1981), failed to resolve the error variance problem although there was a marginal improvement in the models (R^2 lake cages = 0.41–0.46; R^2 rearing channel = 0.84–0.87). The weighted least squares technique (weighting factors from standard least squares regression) (Table 4) indicated significant differences among growth functions of the three units for each rearing method. Variability in growth response of parr of the lake cages was greater than for those in mesh troughs. Rate of increase in total parr length (slope) was greater among parr in mesh troughs than in lake cages. It appears that average growth performance was best for parr of the intermediate-density treatment for lake cages in 1984 and for the low-density mesh trough treatment.

Regression of weight on length (log–log transformed) for the 1984 experiments indicated that the condition of parr was significantly different among units (Table 5) within each rearing method. Adjusted mean weights for these regressions suggest that parr in the mesh troughs had a higher average weight per unit total length than those in the lake cages. Within each rearing method, parr condition was greatest for the high-density groups.

Discussion

There is considerable literature to indicate that fry feeding and hatchery technology has been pursued on a global basis since at least the 1800s (MacCrimmon et al. 1974) and that hatchery methods are effective in producing salmonids (Bardach et al. 1972). In contrast with high technology hatchery applications, we are confining our fall-fingerling salmon rearing experiments mainly to less complex seminatural applications involving rearing channels and lake cages and to natural lacustrine and riverine habitats.

Our present interest in fall-fingerlings stems largely from the findings of MacCrimmon (1954) who documented significant trout predation on salmon fry, from Warner (1972) who found that brook trout (*Salvelinus fontinalis*) did not prey on stocked 1+ salmon parr, and from Fraser (1978) who recommended stocking of fall-fingerling brook trout in the presence of resident competitors. The apparent susceptibility of swim-up fry to predation suggests that parr stages may have increased survival potential as demonstrated by Elson (1959). We are concerned also about potential behavioral differences between wild fry and those reared on artificial diets. In apparent contrast with his 1959 results, Elson (1975) hypothesized that newly planted hatchery underyearlings are less aggressive than wild resident juveniles and therefore are displaced from suitable stream habitat where stocking results in sympatry. This speculation has been supported by Dickson and MacCrimmon (1982). The apparent behavioral inferiority of hatchery relative to wild fry, together with increased survival of fall-fingerlings, in stream habitats suggests that size at release and timing of release may be key factors in developing stream enhancement strategies.

While resident brook trout are piscivorous at sizes greater than 15 cm (Clemens 1928) and act as predators on juvenile salmon (MacCrimmon 1954), we expect that fall-fingerlings, stocked directly into littoral lake habitats containing trout, will be large enough to avoid excessive predation (Warner 1972). With respect to timing of release of juvenile salmon to freshwater habitats, predation and competition in lacustrine habitat is expected to be lower in the fall than at the time of normal swim-up fry migration. Most mature resident brook trout have emigrated from Newfoundland lakes by late September and are preoccupied with spawning at this time. This implies that they are spatially and physiologically unlikely to exert significant predation on young salmon distributed to lacustrine habitats.

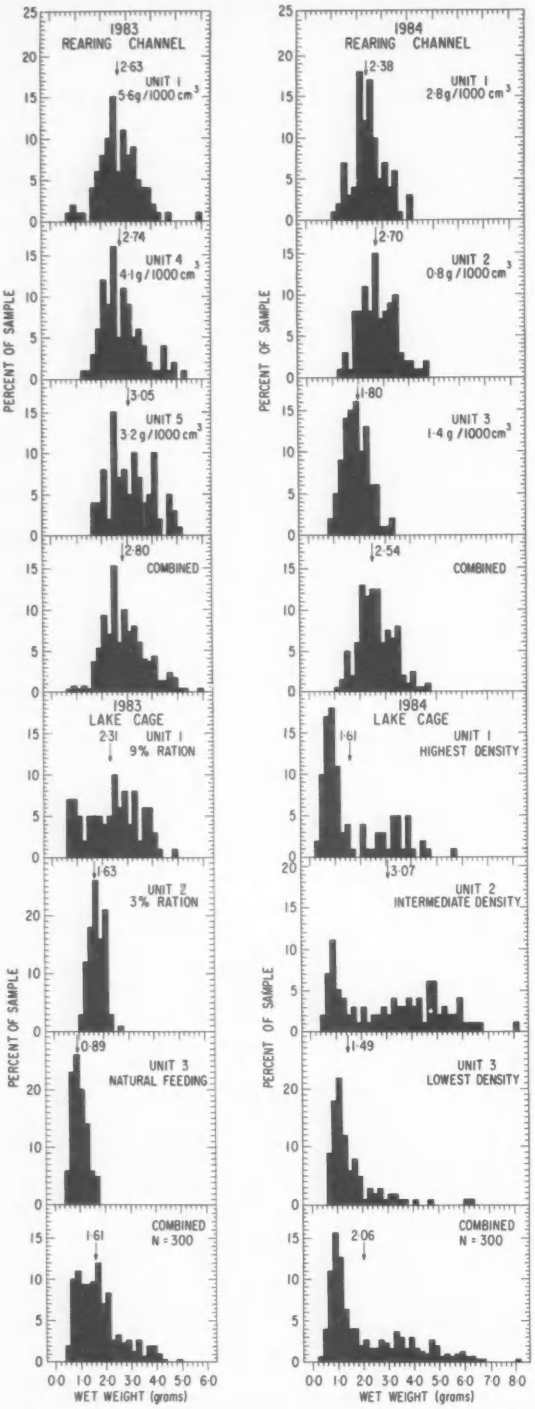

FIG. 5. Final size histograms for fall-fingerling Atlantic salmon raised in seminatural culture experiments.

Predation from immature brook trout and from postyearling salmon parr at this time also is expected to be minimal due to decreasing water temperature (about 5°C in early October), which is known to reduce salmonid feeding intensity (Allen 1940, 1941; Gibson 1978). To warrant continued effort toward fall-fingerling production, the level of early rearing mortality associated with our relatively uncontrolled rearing conditions will have to be lower than mortality due to predation when fry are released to natural habitats.

Mortality in our rearing channel mesh troughs correspond with the order in which troughs were filled in the 1983 experiments (i.e. trough 1 had the highest mortality and trough 6 had the lowest). In addition, troughs that were filled first had the highest start density. This suggests that density in our 1983 experiments may have been a factor that contributed to high early mortality. This observation is confounded by the fact that the first fry to emerge from the spawning channel in 1983 had varying amounts of yolk sac still present. Early emergence suggests that these first fry may have been "inferior" relative to those that migrated later. This may account partially for the higher survival rates seen in the later units.

Lack of environmental control in our rearing experiments caused several setbacks in anticipated growth performance, especially in the early weeks of rearing experiments. The main focus of these setbacks was daily fluctuation of water temperature (i.e. often ranging from 10°C in the morning to 22°C by midnight). Temperatures as high as 25°C cause noticeable changes in parr behavior and appear to be stressful. Increased stream discharge following heavy rainfall also appears to slow down feeding activity of Atlantic salmon parr. Discoloration of many of Newfoundland's freshwaters following heavy rainfall, due to bog outwash, is a common occurrence throughout the summer. This water discoloration has been accompanied by reduced feeding intensity among parr in our rearing experiments although this may have been simply a function of impaired visual acuity and not physiological distress.

Water chemistry, especially minerals such as calcium and sodium, also may have contributed to suboptimal growth and to elevated mortality in the early, free-swimming life history stage (Bua and Snekvik 1972; Brown and Lynam 1981; Piper et al. 1982; Rodgers 1984). Relatively soft Newfoundland freshwaters likely augment the effects of handling stress in our early rearing of Atlantic salmon. Wedemeyer (1972) and Nakinmaa et al. (1983) showed that the physiological consequences of handling stress could be decreased by addition of salt to the water. Dissolved calcium can be adsorbed directly from surrounding water (Phillips et al. 1963) for structural purposes. Sharp termination of the early rearing mortality problem, following the salt baths, supports the suspicion that water chemistry may be an important limiting factor in seminatural rearing of Atlantic salmon parr.

Coping with problems of lack of environmental control under seminatural rearing conditions has been a matter of accepting the inevitable. Without environment control of temperature and water chemistry, the practice that has developed in our experiments has been to stop providing food to parr during extremes of environmental conditions, thereby lowering the metabolic demands of digestion (Ivlev 1961; Kerr 1971). We conclude, from our records of diurnal fluctuations in water temperature, that feeding schedules that revolve around normal work days (i.e. 09:00–17:00) may not be conducive to obtaining maximum growth potential under semi-

TABLE 5. Weight – total length regression parameters for 1984 salmon parr rearing experiments.

Method	Unit	Density (g/100 cm³)	Regression parameters		Regresion slopes		Mean length (cm)[a]	Mean weight (g)[a]	Adjusted mean weight (g)	N
			Intercept	Slope	F	P				
Mesh	1	2.8	−5.3739	3.1892	4.03	0.0179	5.35	2.7	2.6	600
trough	2	0.8	−5.3388	3.1656			5.48	2.9	2.6	600
	3	1.4	−5.2551	3.1173			5.27	2.5	2.6	580
Lake	1	Highest	−5.3215	3.1512	11.94	0.0001	5.11	2.3	2.3	580
cage	2	Intermediate	−5.1772	3.0665			5.43	2.8	2.8	580
	3	Lowest	−5.0830	3.0083			5.27	3.0	2.3	580

[a]Transformed from log parameters.

natural conditions. At the Indian Brook research station, water temperature usually is lowest during the early morning and rises throughout the afternoon to peak before midnight. Lower water temperatures in the morning do not seem to retard feeding intensity. Therefore, it is likely that daily food intake could be increased if feeding schedules were maintained beyond the end of the normal work day. Automatic feeders, if used from the end of the work day until shortly before dusk, would make better use of daylight hours to secure parr growth.

Swim-up fry (Arnemo et al. 1980) and parr (Thomas 1962; Arnemo 1975) have been observed to eat zooplankton, and our experiments confirmed this for caged parr. This appears to be advantageous during the early rearing phase. The 1983 experiments, in which swim-up fry were left virtually unattended during the first 40 d, indicated a major saving in effort required to bring these parr through the first feeding phase. When compared with the effort required at the rearing channel, where hand-feeding, mesh cleaning, and salt baths were essential to control mortality, advantages of natural zooplankton food sources are evident. However, lake cage experiments also reveal that natural zooplankton diets are not adequate in themselves to maintain good growth characteristics among parr. Results of our 1984 experiments indicate that there is an interaction effect between natural zooplankton and artificial food in that parr, in the cage receiving the greatest quantity of artificial food, also consumed the greatest amount of zooplankton. It appears that zooplankton are attracted into lake cages, possibly either by the presence of the artificial food or by the increased amounts of detrital material accumulating in these cages. Experiments by Holm et al. (1982) demonstrated the feasibility of providing diet supplements to caged parr by pumping zooplankton to the cages from nearby lake areas. While such an approach may have resulted in reduced fouling of our cages due to reduce detrital accumulation, the nutritional quality of the diet of parr in the lake cages that received supplemental feeding likely was better than that of the natural feed cage. Improved growth performance in the artificial food supplement groups may in fact justify the additional effort required to maintain cage hygiene in artificial feeding situations. An additional concern is that not all lakes have zooplankton production as high as we observed.

Reliance on natural lake zooplankton to initiate first feeding requires a priori consideration of zooplankton species composition and abundance. Where species composition and abundance is adequate, it appears that zooplankton stimulate a feeding response that generates heightened appetite and better growth performance. It appears also that parr develop preferences for certain species of zooplankton although this preference varies somewhat from one parr to another. Zooplankton sampling of lacustrine areas somewhat removed from the cage site, together with examination of stomach contents, suggests that parr may have been selective for *Daphnia catawba* and that some species (i.e. *Sida crystallina*) may not have been as attractive to parr. *Diaptomus minutus* is particularly interesting in that it was more abundant within the cages than outside and yet was not found in any parr stomachs. Zooplankton species that were not common either in the lake cages or among stomach contents may not have been equally attracted to the cage environment, and indeed may have avoided cages due to chemical stimuli resulting from detrital accumulation and decomposition. However, we do not favor this hypothesis because parr in the natural feed cage had the same basic zooplankton incidence among stomachs as parr that received supplemental artificial feeding.

A concern with semiwild rearing experiments to date relates to the variability in final size among parr in lake cages. It is apparent that the range of sizes of parr at the end of the lake cage experiments is much larger than for the mesh troughs. The apparent bimodality in size of lake cage parr, which is not as pronounced among parr in the rearing channel experiments (Fig. 5), may indicate competition for resources (food and/or space) within lake cages or may reflect different preferences among parr within any one cage for the two types of food available to them. Lake cages have a much more pronounced depth dimension that prevents routine observation of parr behavior and interaction. The opportunity to observe feeding intensity and food selectivity in the mesh troughs, and the effort applied to manual feeding in this situation, allows the rearing technician to select the most appropriate type of food to use, the rate at which artificial diets should be dispensed, and when to stop introducing food. Lake cages do not provide this opportunity.

Assuming that zooplankton enter the lake cage largely through the sides of the net, parr located closest to the net would have the best chance to consume this prey; consequently, parr toward the center of the net would have a much reduced opportunity to feed on zooplankton. Unfortunately, the artificial feeding apparatus used in these experiments, in spite of our attempts to discharge food homogeneously, also ensures disproportionate feeding intensity within the cage. The distribution mechanism of the automatic feeders is a louvered spinning disk for spraying food around the interior of the cage. Although artificial food was distributed over the entire surface of the lake cage, much of this food was observed to bounce off the top edges of the net, thereby encouraging greater food abundance at the periphery of the lake cage.

Tables 4 and 5 and Fig. 5 suggest growth and condition advantages among parr reared in mesh troughs relative to those reared in the lake cages. We suspect this reflects the much greater amount of attention given to the rearing channel experiments and also to problems experienced with the automatic feeders that were used on the lake cages. Occasionally these feeders did not dispense food at the timed intervals or, conversely, dispensed far too much food at one time.

Although we expect that lake cage rearing techniques for parr can be devised to overcome the disparity observed in growth characteristics between the two seminatural rearing options we used, our best parr growth is lower than the 4.7%/d achieved by Thorpe et al. (1982) under hatchery conditions. We consider such a growth rate to be an unrealistic goal for our ongoing experiments with seminatural rearing techniques in Newfoundland but do hope to reach a growth rate of 3.5%/d (to give a 4- to 5-g fall-fingerling). To date, our seminatural rearing experiments have indicated a growth advantage over natural Indian Brook habitat. Relative to final mean weight, this advantage has ranged from 2.4 to 4.5 times.

Our experiments have indicated that it is feasible to use semiwild rearing techniques to produce significant numbers of fall-fingerling salmon. However, we have not yet demonstrated the quality of these parr. We do not know how observed growth and survival rates during these experiments relate to the performance of parr subsequent to release. Our results suggest size advantages for seminaturally reared parr relative to wild parr; however, the merits of stocking swim-up fry or fall-fingerlings may vary among different recipient habitats. Although we anticipate heavy mortality among newly distributed swim-up fry in the spring (at a time when resident brook trout are most voracious), we do not know how serious mortality will be for fall-fingerlings immediately following release or how the economics of fry feeding and subsequent survivorship will compare with results of swim-up fry distribution. Pedley and Jones (1978) have shown increased survival by stocking fall-fingerlings, and Havey (1973) found that the survival of stocked yearlings was 2.8 times that for underyearlings. However, Havey (1973) also found that the cost of stocking yearling parr was 4 times the cost of stocking underyearlings. Such comparisons of survival rates and production costs will be the object of our future research in salmon enhancement stocking experiments in Newfoundland. Our long-range salmon experiments are designed to allow objective comparison of parr versus unfed fry stocking and of survival between allopatric and sympatric year-classes.

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References

ALLEN, K. R. 1940. Studies on the biology of the early stages of the salmon (*Salmo salar*). 1. Growth in the River Eden. J. Anim. Ecol. 9: 1–23.

1941. Studies on the biology of the early stages of the salmon (*Salmo salar*). 3. Growth in the Thurso River system, Caithness. J. Anim. Ecol. 10: 273–295.

ARNEMO, R. 1975. Limnological studies in Hyttodammen. The young salmon: its growth and food. LFI MEDD. 5/1975: 86 p.

ARNEMO, R., C. PUKE, AND N. G. STEFFNER. 1980. Feeding during the first weeks of the young salmon in a pond. Arch. Hydrobiol. 89: 265–273.

BARDACH, J. E., J. H. RYTHER, AND W. O. MCLARNEY. 1972. Aquaculture. Wiley Interscience, New York, NY. viii + 301 p.

BLACK, E. C., AND I. BARRETT. 1957. Increase in levels of lactic acid in the blood of cutthroat and steelhead trout following handling and live transportation. Can. Fish. Cult. 20: 13–23.

BROWN, D. J. A., AND S. LYNAM. 1981. The effect of sodium and calcium concentrations on the hatching of eggs and the survival of the yolk sac fry of brown trout, *Salmo trutta* L., at low pH. J. Fish Biol. 19: 205–211.

BUA, B., AND E. SNEKVIK. 1972. Hatching experiments with roe from salmonid fishes, 1966–1971. Effects of acidity and dissolved salt in the water. Vann. 7: 86–93. (Transl. from Norwegian by FBA(NS), No. 80)

CLEMENS, W. A. 1928. The food of trout from the streams of Onida County, New York. Trans. Am. Fish. Soc. 58: 183–197.

DAVIS, J. P., AND M. K. FARWELL. 1975. Exploits River and Indian River Atlantic salmon development programs — 1974. Resource Development Branch, St. John's, Nfld., Internal Report Series No. NEW/I-71-1: 55 p.

DICKSON, T. A., AND H. R. MACCRIMMON. 1982. Influence of hatchery experience on growth and behavior of juvenile Atlantic salmon (*Salmo salar*) within allopatric and sympatric stream populations. Can. J. Fish. Aquat. Sci. 39: 1453–1458.

DRAPER, N. R., AND H. SMITH. 1981. Applied regression analysis. John Wiley & Sons, Inc., Toronto, Ont. 709 p.

ELSON, P. R. 1959. Developing effective use of hatchery-reared Atlantic salmon (*Salmo salar*) in Canada. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 148: 62–71.

1975. Atlantic salmon rivers smolt production and optimal spawning: An overview of natural production. Int. Atl. Salmon Found. 6: 96–119.

FARWELL, M. K., AND T. R. PORTER. 1976. Atlantic salmon enhancement techniques in Newfoundland. FAO Tech. Conf. on Aquaculture, Kyoto, Japan. FIR:AQ/Conf/76/E.31: 8 p.

FRASER, J. M. 1978. Comparative recoveries of planted yearling and fall fingerling brook trout, *Salvelinus fontinalis*, from Ontario lakes, Canada. J. Fish. Res. Board Can. 35: 391–396.

GIBSON, R. J. 1978. The behavior of juvenile Atlantic salmon, *Salmo salar*, and brook trout, *Salvelinus fontinalis*, with regard to temperature and to water velocity. Trans. Am. Fish. Soc. 107: 703–712.

GOVERNMENT OF CANADA. 1984. Fish health protection regulations manual of compliance. Misc. Spec. Publ. 31 (revised): iv + 39 p.

HAVEY, K. A. 1973. Relative recoveries of hatchery reared landlocked salmon planted at different ages at Schoodic Lake, Maine. Trans. Am. Fish. Soc. 102: 121–124.

HOLM, J. C., T. HANSEN, AND D. MOLLER. 1982. Start feeding of salmonids with lake zooplankton. ICES C.M. 1982/F:36. Maricult. Comm. Anad. and Cat. Comm. 11 p.

IVLEV, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, CT. 302 p.

KERR, S. R. 1971. Prediction of fish growth efficiency in nature. J. Fish. Res. Board Can. 28: 809–814.

KISLALIOGLU, M., AND R. N. GIBSON. 1977. The feeding relationship of shallow water fishes in a Scottish sea loch. J. Fish Biol. 11: 257–266.

LEITRITZ, E., AND R. C. LEWIS. 1976. Trout and Salmon culture (hatchery methods). Calif. Dep. Fish Game Bull. 164.

LEMM, C. A., AND M. A. HENDRIX. 1981. Growth and survival of Atlantic salmon fed various starter diets. Prog. Fish-Cult. 43(4): 195–199.

MACCRIMMON, H. R. 1954. Stream studies on planted Atlantic salmon. J. Fish. Res. Board Can. 11: 362–403.

MACCRIMMON, H. R., J. E. STEWART, AND J. R. BRETT. 1974. Aquaculture in Canada: the practice and the promise. Bull. Fish. Res. Board Can. 188: 84 p.

MAZEAUD, M. M., F. MAZEAUD, AND E. M. DONALDSON. 1977. Primary and secondary effects of stress in fishes: some new data with a general review. Trans. Am. Fish. Soc. 106: 201–212.

NAKINMAA, M., A. SOIVIO, T. NAKARI, AND S. LINDGREN. 1983. Hauling stress in brown trout (*Salmo trutta*): physiological responses to transport in fresh water or salt water, and recovery in natural brackish water. Aquaculture 34: 93–100.

O'CONNELL, M. F., J. P. DAVIS, AND D. C. SCOTT. 1983. An assessment of the stocking of Atlantic salmon (*Salmo salar* L.) fry in the tributaries of the Middle Exploits River, Newfoundland. Can. Tech. Rep. Fish. Aquat. Sci. 1225: v + 142 p.

PEDLEY, R. B., AND J. W. JONES. 1978. Growth and survival of Atlantic salmon (*Salmo salar*) in Llyn Dwythwch, North Wales. Freshwater Biol. 8(5): 423–431.

PEPPER, V. A., N. P. OLIVER, AND R. BLUNDON. 1985. Evaluation of an experiment in lacustrine rearing of juvenile anadromous Atlantic salmon. N. Am. J. Fish. Manage. 5(4): 507–525.

PHILLIPS, A. M. JR., A. V. TUNISON, AND G. C. BALZER. 1963. Trout foods and feeding. U.S. Dep. Inter. Bur. Sport Fish. Wildl. Circ. 159: 36 p.

PIPER, L. G., I. B. MCELWAIN, L. E. ORME, J. P. MCCRAVEN, L. G. FOWLER, AND J. R. LEONARD. 1982. Fish hatchery management. U.S. Department of the Interior, Fish and Wildlife Service, Washington, DC. 517 p.

PRATT, J. D. 1968. Spawning distribution of Atlantic salmon (*Salmo salar* L.) in controlled flow channels. M.Sc. thesis, Biology Department, Memorial University of Newfoundland, St. John's, Nfld. 143 p.

PRATT, J. D., M. K. FARWELL, AND H. J. RIETVELD. 1974. Atlantic salmon production using a spawning channel. Rep. Ser. No. NEW/I-74-7: 29 p.

RODGERS, D. W. 1984. Ambient pH and calcium concentration as modifiers of growth and calcium dynamics of brook trout, *Salvelinus fontinalis*. Can. J. Fish. Aquat. Sci. 41: 1774–1780.

SLANEY, P. A., AND W. L. HARROWER. 1981. Experimental culture and release of steelhead trout reared in net-pens at O'Connor Lake in British Columbia. *In* T. J. Hassler [ed.] Proc. Symp. Propagation, Enhancement, and Rehabilitation of Anadromous Salmonid Populations and Habitats. Humboldt State University, Arcata, CA. 13 p.

STURGE, C. C. 1968. Production studies on the young stages of Atlantic salmon (*Salmo salar* L.) in an experimental area of Indian River, Notre Dame Bay, Newfoundland. M.Sc. thesis, Biology Department, Memorial University of Newfoundland, St. John's, Nfld. 134 p.

THOMAS, J. D. 1962. The food and growth of brown trout (*Salmo salar* L.) and the eel (*Anguilla anguilla* L.) in the River Teify, West Wales. J. Anim. Ecol. 31: 175–205.

THORPE, J. E., C. TALBOT, AND C. VILLARREAL. 1982. Bimodality of growth and smoltifying in Atlantic salmon, *Salmo salar* L. Aquaculture 28: 123–132.

WARNER, J. 1972. Further studies of fish predation on salmon stocked in Maine lakes. Prog. Fish-Cult. 34(4): 217–221.

WEDEMEYER, G. 1972. Some physiological consequences of handling stress in the juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 29: 1780–1783.

WEDEMEYER, G. A., R. L. SANDERS, AND W. C. CLARKE. 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmon. Mar. Fish. Rev. 42(6): 1–14.

ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, NJ. 620 p.

Critical Swimming Speed of Fraser and Thompson River Pink Salmon (*Oncorhynchus gorbuscha*)

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Williams, I. V., and J. R. Brett. 1987. Critical swimming speed of Fraser and Thompson River pink salmon (*Oncorhynchus gorbuscha*).Can. J. Fish. Aquat. Sci. 44: 348–356.

Critical swimming speeds were determined for male and female pink salmon (*Oncorhynchus gorbuscha*) captured from the Fraser and Thompson rivers and Seton Creek, British Columbia. The fish were categorized into two basic groups. Lower river fish were captured from the Fraser River at Fort Langley and Yale, and up-river fish were captured from the Thompson River at the Canyon and at Ashcroft and from Seton Creek near Lillooet, British Columbia. The critical swimming speeds of males and females in various stages of maturation were compared. In general, the up-river fish were stronger swimmers than the lower river fish. Gravid fish were stronger swimmers than spawning fish, which in turn were stronger swimmers than fish which were spawned out. Standardized critical swimming speeds ranged from a mean of 1.73 ± 0.35 (SE) body lengths/s for spawned females up to 3.39 ± 0.48 lengths/s for up-river gravid males.

On a déterminé les vitesses de nage critique chez des saumons roses (*Oncorhynchus gorbuscha*) mâles et femelles capturés dans le fleuve Fraser, la rivière Thompson et le ruisseau Seton (Colombie-Britannique). Les poissons ont été séparés en deux catégories : ceux d'aval capturés dans le fleuve Fraser à Fort Langley et Yale et ceux d'amont capturés dans la rivière Thompson à Canyon et Ashcroft et dans le ruisseau Seton près de Lillooet. On a ensuite comparé les vitesses de nage critique chez les mâles et les femelles à divers stades de maturité. En général, les poissons d'amont sont de plus puissants nageurs que ceux d'aval. De plus, les poissons pleins sont plus vigoureux que les poissons frayants; ceux-ci sont par contre plus robustes que les poissons vides. Les vitesses de nage critique normalisées varient d'une moyenne de 1,73 ± 0,35 (ET) longueur du corps/seconde chez les femelles vides à 3,39 ± 0,48 longueurs/s chez les mâles pleins d'amont.

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The possibility of encroachments into migration and spawning areas of anadromous salmonids caused by the continuing construction of the CN twin track from Valemont to Vancouver, British Columbia, has raised some serious questions regarding the salmon runs to the Thompson River (Federal Environmental Assessment Review Office 1983). An examination of pink salmon (*Oncorhychus gorbuscha*) swimming capacity was undertaken in 1983 because pinks are considered to be the weakest of the anadromous salmonids and therefore most subject to any adverse affects of altered river velocities (Brett 1982).

One of the basic concerns involving the disruption of migration paths of salmon is the possibility of the salmon having insufficient energy reserves to overcome any imposed changes. Pink salmon do not eat once they enter the Fraser River; therefore, they have a limited supply of energy to fuel their migration and spawning activities.

The major factors affecting rates of energy expenditure are swimming speed, weight, and temperature. While there is a good scientific basis for sockeye salmon (*Oncorhynshus nerka*) (Brett 1967; Brett and Glass 1973), there is a paucity of information on pink salmon (Beamish 1978; Lister 1981).

The swimming speed of pinks with a mean length of 64 cm in the Pacific Ocean was reported to range from 23 to 78 cm/s (Stasko et al. 1973). Krykhtin (1964, cited in Malinun 1973) reported a mean swimming speed of 55 cm/s at 5–6°C for pinks in the Amur River, USSR; however, no lengths were reported. Therefore, as a part of a broad research program on the upstream migration of pink salmon in the Fraser River, a study to determine their critical swimming speeds was begun in the fall of 1983.

The critical swimming speed (U_{crit}), approximately the maximum sustained swimming speed of the fish (see definition of terms in Brett 1982), is an essential part of the information needed to establish the active metabolic rate. When a fish reaches its maximum swimming speed, the accompanying maximum oxygen uptake is termed active metabolism (M_a). These factors plus the determination of the standard metabolism (M_s) allow an estimate of energy utilization, given a known swimming speed. Knowledge of the critical swimming speed also helps to define portions of the river where velocity exceeds the sustained speed requiring burst speeds. Because burst speeds exceed the energy provided by M_a, they are of short duration (20 s or less) and result in oxygen debt. This state

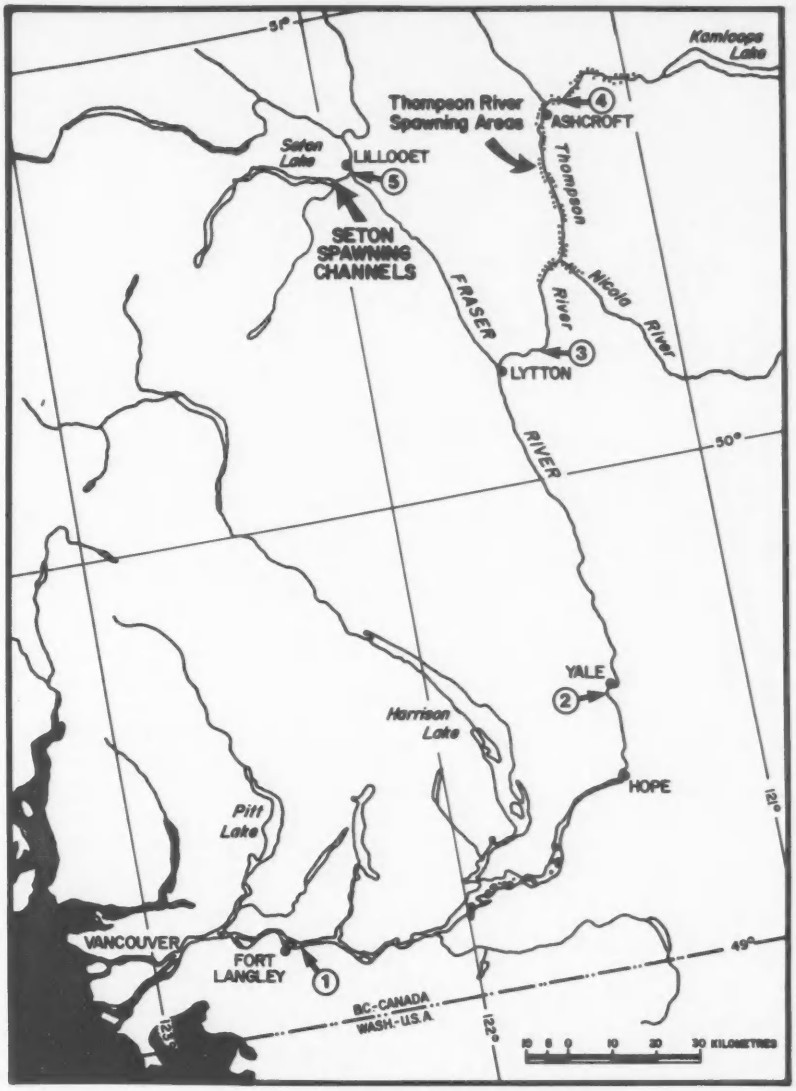

FIG. 1. Capture sites for 1983 pink salmon study.

of fatigue requires rest periods to reestablish normal swimming ability. These data can then be used to enhance prediction of the consequences from changed river passage.

Materials and Methods

Fish

Pinks from five locations were tested at Seton Creek. They were captured from the captured from the Fraser River at Fort Langley and at Yale, from the Thompson River at the Thompson Canyon near Lytton and at Ashcroft, and from the Seton Power Project tailrace, near Lillooet, BC (Fig. 1). The capture and transport methods are detailed in Williams et al. (1986).

Upon arrival the fish were placed in one of three holding pens each measuring approximately 3×8 m and held a minimum of 24 h. Most of the pinks paired off and began exibiting spawning behaviour very soon after placement in the holding pens.

Swimming Test Apparatus

The test apparatus, in the form of parallel tunnels, was installed in the upper end of the upper spawning channel at Seton Creek (Copper 1977), near Lillooet. A small dam (flow control weir) was constructed across the top of the channel just downstream of the water intake. This provided the head required to produce tunnel velocities in excess of 1.5 m/s.

Eight tunnels, each 30 cm inside diameter, were inserted through the bottom of the dam. Each tunnel was 11 m long with a 1.8-m clear plastic (acrylic) section installed 6 m from the top end of the tunnel. A fixed screen of vertical aluminum plates

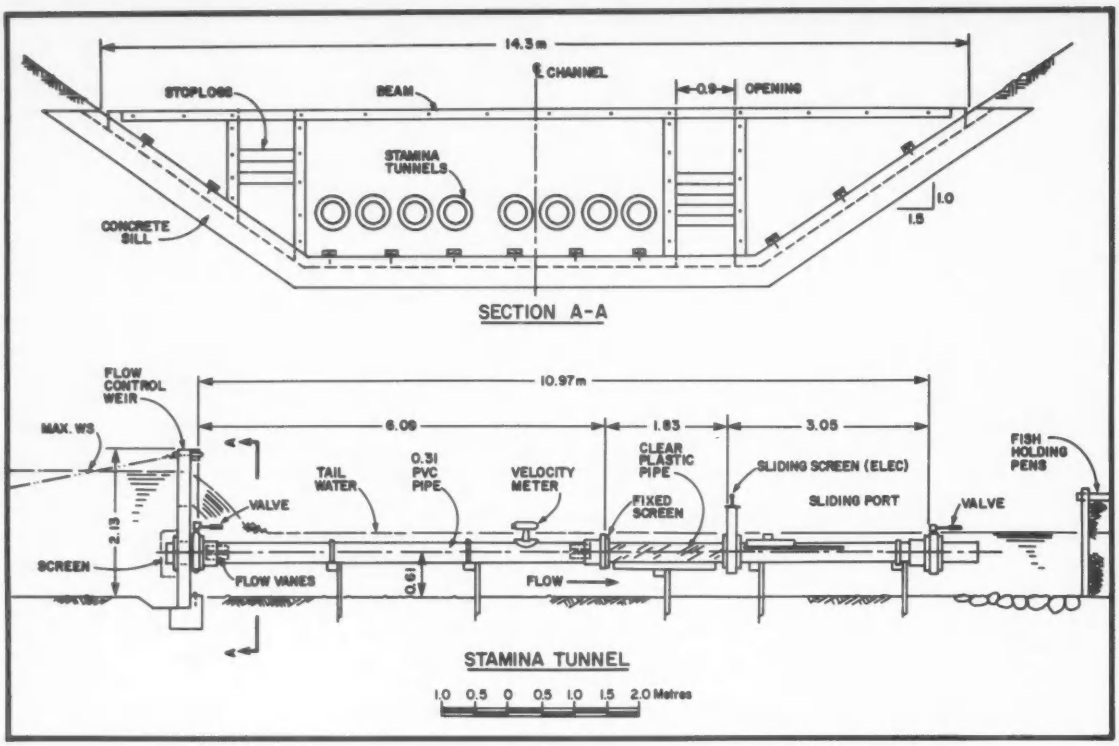

FIG. 2. Critical swimming test apparatus installed in the upper Seton spawning channel.

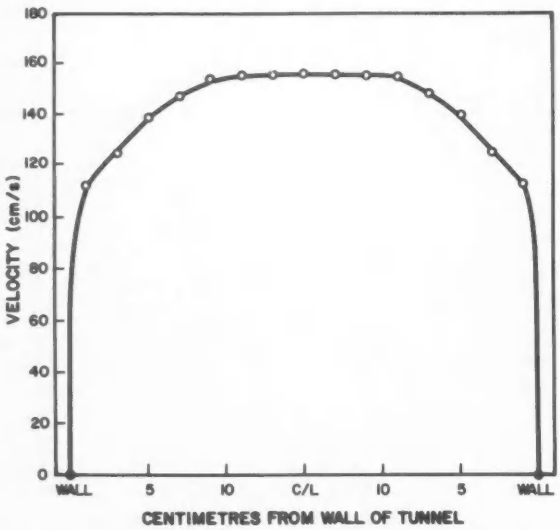

FIG. 3. Water velocity profile in the test tunnels at 150 cm/s.

was placed just upstream of the acrylic, and a removable screen which was charged with electricity during swimming speed testing was installed at the lower end of the acrylic section. A butterfly valve was installed at the upper end of the tunnel, close to the dam, and another was installed at the downstream end of the tunnel. The velocities were controlled by use of a combination of these valves and adjusting stop logs in the flow control weir (Fig. 2).

Velocities were measured with Gurley–Price flowmeters installed in each tunnel approximately 1 m upstream from the clear acrylic pipe. In addition a probe meter (Monitek FloProbe magmeter) was also installed 60 cm upstream of the Gurley meter in tunnel 8 only. Velocities were determined in the cross-sectional area of the tunnels (Fig. 3) and the meter was installed so that the velocity 5–6 cm from the tunnel wall was measured. This was somewhat lower (8%) than maximum velocity at the higher velocities (Fig. 3). The individual Price meters were calibrated with the probe meter.

Fish were loaded through a port located approximately 45 cm downstream of the lower screen. Wooden partitions had to be constructed between tunnels because behavioural interactions, caused by visual contact between fish, interfered with the tests.

Experimental Techniques

Critical swimming speed tests were conducted throughout 24 h/d. Fish selected from each group at random were carried and loaded into the tunnels using waterproof vinyl bags in the form of a folding stretcher. The fish were allowed to acclimate for 1 h at 15 cm/s. While many investigators allow greater than a 12-h acclimation, this has been shown to be unneccesary for young coho (*Oncorhynchus kisutch*), as Glova and McInerny (1977) were unable to show any significant difference between 1- and 12-h acclimations.

TABLE 1. Location and number of pinks captured at the five sample sites for swimming tests.

Date	Location	No. tested: Males	No. tested: Females
Sept. 11	Ft. Langley	21	24
16	Ft. Langley	16	23
23	Ft. Langley	28	21
Total		65	68
Sept. 26	Yale	17	31
28	Yale	25	25
Total		42	56
Sept. 30	Thompson Canyon (Lytton)	24	28
Oct. 5	Ashcroft	4	28
6	Ashcroft	18	44
Oct. 5	Seton (Lillooet)	5	6
10	Seton (Lillooet)	31	29
Total		36	35
Overall total		189	259

Stepwise increases in velocity lasting 30 min were used to determine the critical swimming speed. Tests were started at 30 cm/s and the velocities were increased approximately 10−15cm/s for each 30-min step until the fish fatigued. A few tests were run with steps of 60 min to allow comparison with previous data (Brett 1982). Water temperatures were recorded for each test.

Velocities in all tunnels were adjusted simultaneously. Tail beat frequencies were recorded for each fish during each step. The time to exhaustion was recorded. The exhausted fish were then removed, killed, and tagged for identification. The maturity of each female pink was classified as gravid (tight egg skeins), spawning (loose eggs from 10 to 90%), and spawned out (0 to 10% eggs). Males were more difficult to classify; however, an attempt was made to differentiate between the stages of maturity. Males that did not leak milt easily were classified as gravid, while those that did were classified as spawning. Physical measurements taken on each fish included total length (TL), fork length (FL), and standard length (SL). The maximum depth and width of each fish was measured and the maximum cross-sectional area was recorded by cutting the fish vertically in its midsection and stamping an impression on blank paper. The cross-sectional area was then measured with a planimeter.

Total fish weights and gonad weights were determined for each fish. A piece of female gonad was preserved in 10% formalin. Fecundities, egg size, and dry egg weights were determined for gravid females, and egg size and egg weights were determined for spawning females. Each fish was examined for any obvious signs of physical disability.

Swimming Speed

The swimming speed of fish tested in tunnels is subject to various influences due to the restricted space in the tunnel. The most significant factors are horizontal buoyancy, solid blocking, and propeller corrections. The horizontal buoyancy adds to drag. The propeller correction is opposite in effect, approximately cancelling the horizontal buoyancy effect (Webb 1975). For this study it was felt that solid blocking was the only significant factor requiring correction. Correction for the solid blocking effect created by the cross-sectional volume displacement was determined by the formula

$$V_f = V_t(1 + E_s)$$

where V_f = corrected velocity, V_t = test velocity, and

$$E_s = \tau\lambda(A_0/A_t) + E_{1.5}$$

where $\tau = 0.8$, $\lambda = 0.7$ length/thickness, A_0 = maximum cross-sectional area of fish, and A_t = tunnel cross-sectional area.

These formulae are explained by Bell and Terhune (1975). Corrected tunnel velocities were then converted to fish lengths per second to allow comparisons of different-sized fish within a relatively small size range.

The critical velocity (U_{crit}) was calculated from the corrected velocities by the formula

$$U_{crit} = V_1 + (T_{V_F}/T_{V_1} \times V_F - V_1).$$

where V_1 = velocity prior to fatigue, V_F = velocity at fatigue, T_{V_F} = time at V_F, and T_{V_1} = time at V_1.

The U_{crit} was then standardized to 15°C for comparison with other salmonid data by using the formulae developed by Brett and Glass (1973) and D. Furnell and J. R. Brett (DFO, Pacific Biological Station, Nanaimo, B.C., pers. comm.) where

$$\log U_{crit} = A_t + B \log L_t$$

where $A_t = 0.8695 + 0.01707T$, L_t = total length, and T = degrees Celsius.

The assumption was made that temperature changes would affect pinks in a similar way to sockeye. The B constant was then calculated for each fish by

$$B = \log U_{crit} - (0.8695 + 0.01707T)/\log L_t.$$

The log U_{crit} 15°C was then calculated

$$\log U_{crit}\ 15°C = B + 1.12556 \times \log L_t$$

and

$$U_{crit}\ 15°C = 10^{\log U_{crit}\ 15°C}.$$

Tail beat frequencies (TBF) were used to compare the corrected velocities obtained in this test with those obtained in previous tests by Brett (1982). Student's t-test was used to test for differences between sample means (Simpson et al. 1960).

Results

Critical swimming speeds were determined for 189 male and 259 female pink salmon captured over a 30-d period from five locations (Table 1). The gravid males at 49.1 cm SL were somewhat larger than the females at 46.8 cm (Table 2). Pink salmon lengths will be reported as standard lengths. These may be converted to fork and total length with the following regressions developed for each sex from the 1983 data:

Males (n = 100):

$$TL = 5.4518 + 1.0324SL,\ p < 0.001$$
$$FL = 2.4850 + 1.0535SL,\ p < 0.001$$

Females (n = 266):

$$TL = 10.201 + 0.9195SL,\ p < 0.001$$
$$FL = 6.0497 + 0.9788SL,\ p < 0.001.$$

TABLE 2. Physical characteristics of 1983 gravid pink salmon captured for swimming tests.

		Standard length (cm)		Total wt. (g)		Gonad wt. (g)		GSI		Fecundity	
	n	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Males	182	49.3	3.8	1853	481	88.6	29.0	4.87	1.28	—	—
Females	144	46.8	2.4	1595	276	248.0	56.9	15.40	2.3	1421	282

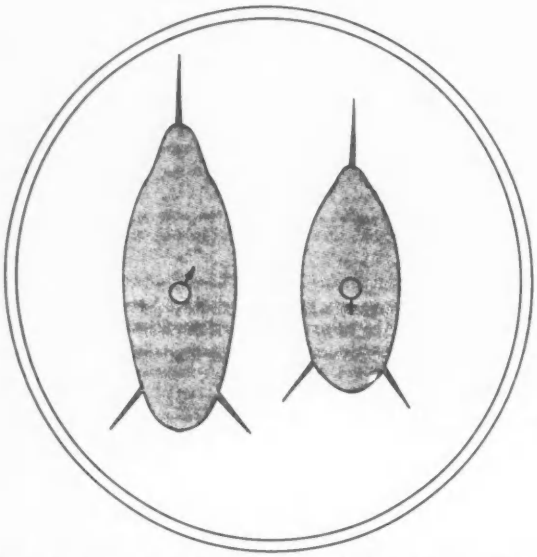

FIG. 4. Cross-section of swim tunnel and pink salmon showing relative sizes of tunnel and male and female pink salmon (only one fish in tunnel during tests).

The mean gonad weight for the males was 88.6 g giving a mean gonadosomatic index (GSI) of 4.87. The female gonads averaged 248 g, with a fecundity of 1421 eggs. The mean GSI for gravid females was 15.4 (Table 2).

The formula used to correct for solid blocking obviously corrected for different form drag (different cross-sectional areas) and also surface drag (shapes of the pinks). That is, the males with the greater cross-sectional area and more pronounced secondary sexual characteristics (i.e. large hump) (Fig. 4) had similar tail beat frequencies as females while swimming at the same relative speed (corrected for solid blocking and expressed as body lengths per second). While the males did have a slightly higher TBF at the higher velocities, in fact, the *t*-test indicated no difference between the male (TBF_m = 50.65 + 48.16 BL/s) and female (TBF_f = 50.85 + 46.73 BL/s) regressions for tail beats per minute versus corrected velocity (t = 0.000012). Therefore, the male and female data were combined. The regression from these data provides a very tight fit of the 99% confidence limits about the line TBF = 50.45 + 47.28 BL/s (Fig. 5A). This allows a high degree of predictability (Figure 5B). Figure 5B allows a comparison of the 1983 data with data that were collected on the Cheakamus pink salmon in 1963 (Brett 1982). These data indicate that the TBF of the Cheakamus River pinks fall within the 95% predictability limits of the 1983 Fraser tests (Fig. 5B).

Water temperature directly affects the swimming performance of fish (Beamish 1978). Water temperatures at the outlet of the test apparatus varied from 13.6°C at the beginning of the season to 10.5°C at the end. Most of the tests were conducted within a 2° range from 10.5 to 12.5°C (Fig. 6). While there is no direct evidence of the effect of temperature

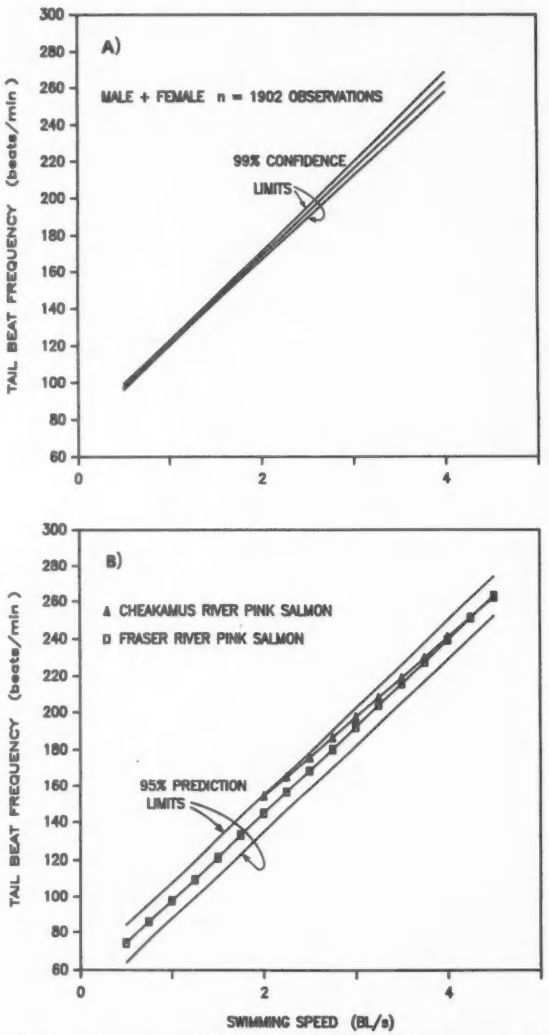

FIG. 5. (A) Regression of tail beat frequency on swimming speed for Fraser pink salmon showing the 99% confidence limits; (B) regressions of tail beat frequency and swimming speed for Cheakamus and Fraser pink salmon. Showing the 95% prediction limits for the Fraser data.

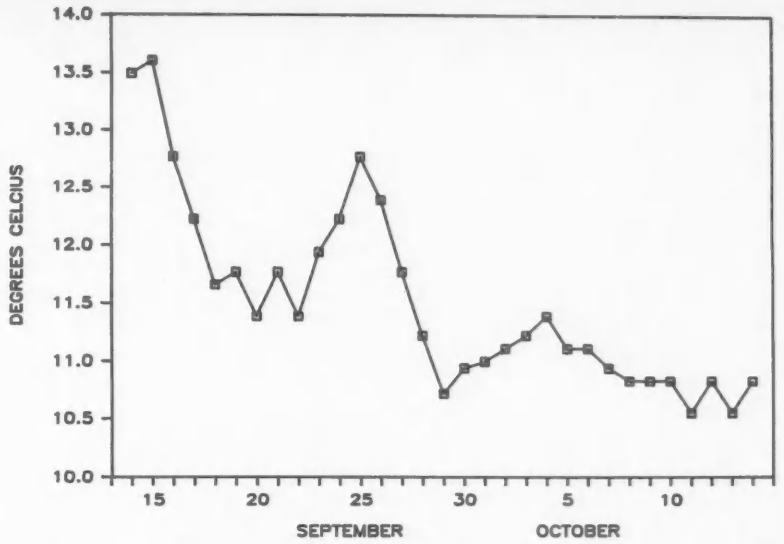

FIG. 6. Mean water temperature measured at the outlet of the test apparatus in the upper Seton spawning channel.

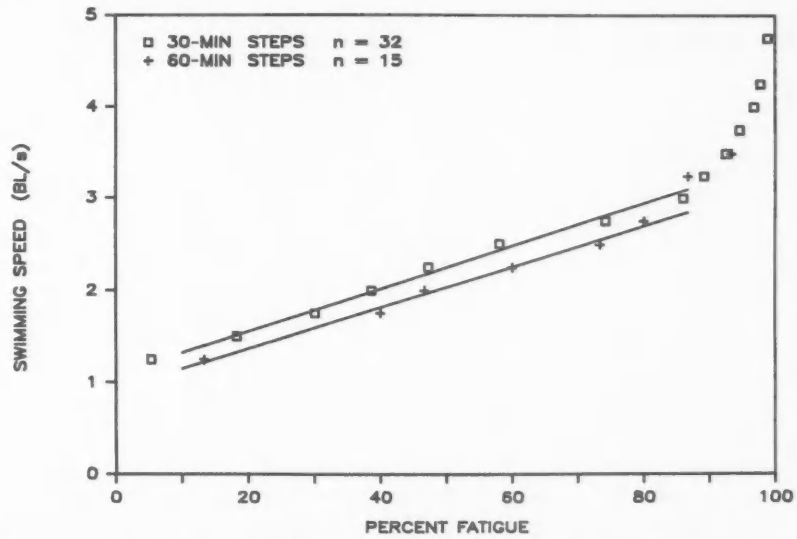

FIG. 7. Regressions of swimming speed and percent fatigue for 30- and 60-min tests (regression based on data from 10 to 80%).

on pink salmon swimming speed, there is a good data base for sockeye salmon (Brett and Glass 1973). As temperatures increase, the swimming performance of sockeye increases to a maximum at 15°C. Therefore, the critical swimming speeds were corrected to a standardized 15°C. These were examined for differences in U_{crit} between the two acceleration periods (60 and 30 min). The majority of the fish used for the tests with 60-min stepwise velocity increments were captured at Fort Langley with a few from Yale (down-river sites). No up-river fish were tested with 60-min increments. The differences between mean U_{crit} 60 and mean U_{crit} 30 for males and females are not statistically significant (Table 3); however, based on the sockeye data of Brett (1982), the U_{crit} 60 should be slightly lower than the U_{crit} 30.

Regression analysis of the relationship between the corrected swimming speeds expressed as body lengths per second and the cumulative percent fatigued indicates that there is a difference between the 60- and 30-min steps at levels of fatigue between 10 and 80% (Fig. 7). Therefore, the 30-min swimming speeds were adjusted to 60-min values by a reduction of approximately 0.2 BL/s. These adjusted data were then examined for differences (Student's t-test) between sexes, state of maturity, capture location, capture dates, holding time prior to testing, tests conducted in natural light (day) and artificial light (night), and

TABLE 3. Comparison of the U_{crit} of gravid pinks tested with 60- and 30-min stepwise velocity increments; all fish from Langley and Yale.

Duration of increment (min)	Males				Females			
		Mean	BL/s			Mean	BL/s	
	n	temp. (°C)	Mean	SD	*n*	temp. (°C)	Mean	SD
30	78	12.1	2.4	0.75	101	12.1	2.2	0.87
60	25	12.4	2.3	0.57	15	12.4	2.2	0.76

TABLE 4. Physical measurements of the male and female pinks by group. L−Y = Langley and Yale; T−A−S = Thompson, Ashcroft, and Seton.

Capture location	Stage of maturity	*n*	Standard length (cm)		Total weight (g)	
			Mean	SD	Mean	SD
Males						
L−Y	Gravid	78	49.1	3.9	1796	481
T−A−S	Gravid	17	48.7	2.9	1798	350
All locations	Spawning	65	49.0	3.5	1823	437
Females						
L−Y	Gravid	101	46.5	5.3	1595	298
T−A−S	Gravid	31	46.6	2.2	1590	218
All locations	Spawning	97	46.1	3.2	1498	270
All locations	Spawned	15	47.2	2.2	1361	197

tunnels used during testing.

There was no significant difference found between the U_{crit} of gravid fish from Langley and Yale (down-river sites) or between the U_{crit} of gravid fish from Thompson, Ashcroft, and Seton (up-river sites). There was no significant difference between groups held 1, 2, 3, 4, 5, 10, 11, and 12 d prior to testing within these classifications or between tunnels or between day and night tests. There was no significant difference between any of the groups in the spawning cateogry or between groups in the spawned out category.

Data analysis of fish captured from the same location on different days indicated no significant differences within their categories, with the exception of one group of six males captured September 23 at Fort Langley. This group had a significantly higher U_{crit} at 2.94 BL/s compared with all other Langley males at 2.41 BL/s. These were also slightly larger fish at 50.7 versus 49.3 cm SL for all Langley males; however, correlation analysis indicated no relationship between size and corrected swimming speed expressed as body lengths per second. Females captured the same day had a slightly U_{crit} of 2.29 compared with all other Langley females at 2.23; however, there is no statistically significant difference between these groups. The males captured September 23 could be an early group of the late-run pinks, as there tends to be some overlap in migration times (Ward 1959).

There were strong differences between the combined U_{crit} of the down-river (Fort Langley and Yale, L−Y) groups and the U_{crit} of the up-river (Thompson, Ashcroft, and Seton, T−A−S) groups. There were also strong differences in the U_{crit} of both males and females captured at T−A−S and tested at various stages of maturity. The spawning fish were stronger swimmers than the spawned fish, while the gravid fish were significantly stronger than the spawning fish. There were also differences between the U_{crit} of the males and females in the T−A−S group.

TABLE 5. Standardized 15°C U_{crit} swimming speeds for the 1983 pink salmon. L−Y = Langley and Yale; T−A−S = Thompson, Ashcroft, and Seton.

Capture location	Stage of maturity	Males			Females		
		n	BL/s		*n*	BL/s	
			Mean	SD		Mean	SD
L−Y	Gravid	103	2.34	0.84	116	2.15	0.98
T−A−S	Gravid	17	3.39	0.96	31	2.78	0.81
All locations	Spawning	65	2.34	1.07	97	2.31	0.94
All locations	Spawned	2	2.13	0.62	15	1.73	0.70

TABLE 6. Standardized U_{crit} swimming speeds (BL/s) at various cumulative fatigue levels.

Percent cumulated fatigue	Langley gravid males and females	Ashcroft			
		Gravid		Spawning males and females	Spawned females
		Males	Females		
10.0	1.17	1.78	2.55	1.05	0.83
20.0	1.40	2.00	2.74	1.33	1.01
30.0	1.62	2.21	2.92	1.61	1.19
40.0	1.85	2.43	3.11	1.88	1.37
50.0	2.08	2.65	3.30	2.16	1.55
60.0	2.31	2.87	3.48	2.44	1.72
70.0	2.53	3.09	3.67	2.72	1.90
80.0	2.76	3.31	3.86	3.00	2.08
90.0	2.99	3.53	4.04	3.28	2.26

group.

Therefore, the U_{crit} 60-min swimming speeds were grouped by sex into gravid, spawning, and spawned categories, with the U_{crit} 60 of gravid fish grouped into the combined L−Y group and the combined T−A−S group.

There were no significant differences in size, (weight, length) of males between the different groups or in size of females between groups. The difference between the mean size of the gravid L−Y and T−A−S males was only 0.4 cm and 1 g, while the females had differences of only 0.1 cm and 5 g (Table 4).

There were no significant differences between the mean U_{crit} of spawning males and females at 2.34 and 2.31 BL/s, respectively, and the mean U_{crit} of the gravid males and females from the L−Y group at 2.34 and 2.15 BL/s (Table 5). While the mean U_{crit} are not significantly different between the spawning group and the L−Y gravid fish, the relationship between cumulative fatigue and swimming speeds is different. The regression coefficient for the gravid L−Y group is similar to that for the gravid females and males from the T−A−S group, indicating that the L−Y group as a whole was composed of

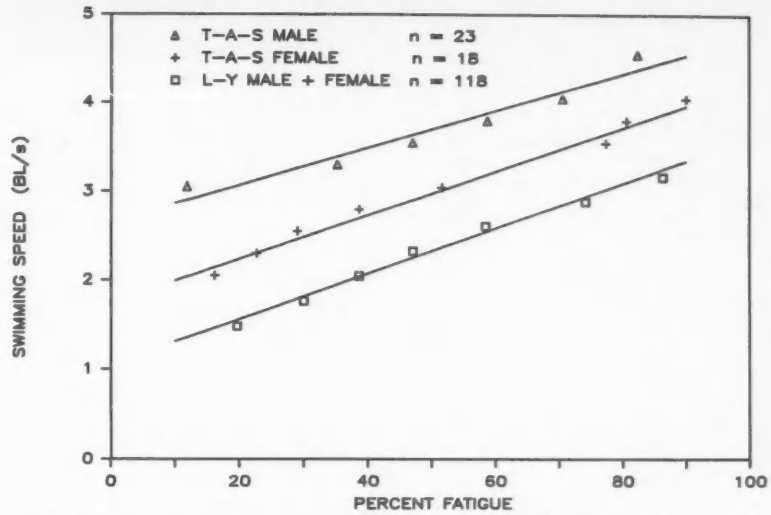

FIG. 8. Regressions of swimming speed versus and percent fatigue for the L–Y and T–A–S fish.

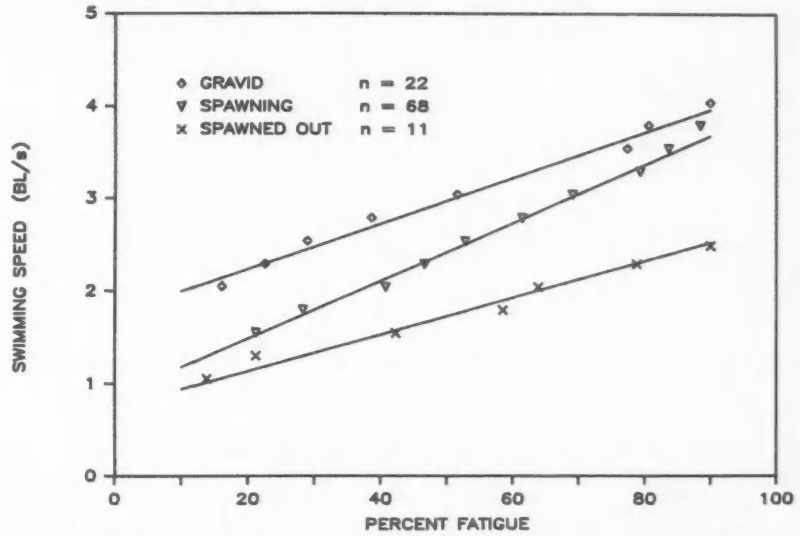

FIG. 9. Regressions of swimming speed and percent fatigue for gravid, spawning, and spawned T–A–S female pinks.

weaker swimmers (Fig. 8). The spawning group has a higher regression coefficient, indicating significantly greater divergence between the poor and good performers (Fig. 9).

The gravid females from the T–A–S group had a significantly higher mean U_{crit} at 2.78 BL/s, while the T–A–S gravid males had the highest at 3.39 BL/s (Table 5). The spawned out females from the T–A–S group had the lowest mean U_{crit} at 1.73 BL/s and a slightly lower slope in the fatigue – swimming speed regression than the gravid fish (Fig. 9).

The U_{crit} swimming speed of the pinks at the cumulative fatigue level of 50% was lower than the mean U_{crit} in every group (Table 6). The 50% fatigue U_{crit} for gravid males and females from L–Y averaged 2.08 BL/s, while the mean U_{crit} averaged 2.15 BL/s. Similarly, the 50% fatigue U_{crit} for the gravid T–A–S males and females, at 3.30 and 2.65 BL/s, respectively, were slightly lower than the mean U_{crit} at 3.39 and 2.78 BL/s.

The free-swimming maximum sustained speed was estimated from the U_{crit} 60-min swimming speeds using the data analysis from fig. 9 in Brett (1982). A comparison of the log time-to-fatigue and the corrected velocities for the Cheakamus pink salmon (Brett 1982) indicates that the maximum sustained swimming speed at the 50% fatigue level was approximately 75% of the 60-min fatigue velocity. Applying this to the 1983 Fraser River data, the free-swimming maximum sustained swimming speed for the gravid L–Y males and females becomes 1.7 BL/s, while that for gravid T–A–S males and females becomes 2.3 BL/s.

Discussion

The analysis of tail beat frequency versus corrected tunnel velocities indicated that the calculated corrected velocities used in this study were very similar to Brett's (1982) empirical corrections using tail beat frequency data from an open flume to correct tunnel velocities (Fig. 5B). It is interesting that while the males tended to have a slightly higher tail beat frequency for a given velocity than the females, the development of a relatively large hump did not handicap the males in a hydraulic sense. That is, there was very little difference between male and female tail beat frequencies at similar swimming speeds expressed as body lengths per second.

The U_{crit} swimming speed of the L−Y group and the spawning pink fall within the data range of pinks captured from the Cheakamus River in 1963 (Brett 1982). However, the U_{crit} for the gravid T−A−S pinks, both males (3.39 BL/s) and females (2.78 BL/s), are significantly higher. The average U_{crit} of 3.08 BL/s for male and female pink salmon is very close to the adult sockeye data (3.1 BL/s) reported by Brett (1973). The difference between the U_{crit} of the lower river fish and the up-river fish cannot be explained by a size difference, as there is no significant difference between the mean lengths (Table 4).

The lower river fish were in transit for a longer period than up-river fish, which may have influenced the test results. However, the lower river fish had similar U_{crit} to the Cheakamus pinks; also, a holding period of 10−12 d prior to testing did not improve their swimming performance. In addition, pink salmon captured at Fort Langley were transported to Bamfield, BC., for metabolism tests. These fish were in transit approximately twice the time of the fish from the lower river which were transported to Lillooet for the U_{crit} determinations, and their U_{crit} swimming speeds (2.22 BL/s for males and females) were very similar to the lower river fish (2.25 BL/s for males and females) (Williams et al. 1986). These data suggest that the influence of the capture and transport is not a major factor in the different swimming performance levels from the upper and lower river fish.

Another possible explanation for this phenomenon is that the Fraser River and the Thompson River canyons, under certain river conditions, select out the weaker swimmers, thus favouring an up-river population of stronger swimmers. Clearly, further work is required to explain the differences in swimming ability between the L−Y pinks and the T−A−S pinks.

This study corroborates Brett's (1982) observation that pink salmon performance is consistently lower than adult sockeye. Adult sockeye from the Stamp River had a free-swimming maximum sustained speed of 2.5 BL/s (Brett 1967). This represents a 14% increase over the gravid up-river pink salmon from this study and a 19% increase over the Cheakamus pinks. The data also indicated that pink salmon swimming performance deteriorated at the advanced stages of maturation. The results therefore indicate that pink salmon would be more sensitive to disruptions of their migratory pathway.

Acknowledgements

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References

BEAMISH, F. W. H. 1978. Swimming capacity, p. 101−175. *In* W. S. Hoar and O. J. Randall [ed.] Fish physiology. Academic Press, New York, NY.

BELL, W. H., AND L. D. B. TERHUNE. 1970. Water tunnel design for fisheries research. Fish. Mar. Serv. Tech. Rep. 195: 69 p.

BRETT, J. R. 1967. Swimming performance of sockeye salmon (*Oncorhynchus nerka*) in relation to fatigue, time, and temperature. J. Fish. Res. Board Can. 24: 1731−1741.

1973. Energy expenditure of sockeye salmon, *Oncorhynchus nerka*, during sustained performance. J. Fish. Res. Board Can. 30: 1799−1809.

1982. The swimming speed of adult pink salmon, *Oncorhynchus gorbuscha*, at 20°C and a comparison with sockeye salmon, *O. nerka*. Can. Tech. Rep. Fish. Aquat. Sci. 1143: 37 p.

BRETT, J. R., AND N. R. GLASS. 1973. Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. J. Fish. Res. Board Can. 30: 379−387.

COOPER, A. C. 1977. Evaluation of the production of sockeye and pink salmon at spawning and incubation channels in the Fraser River system. Int. Pac. Salmon Fish. Comm. Prog. Rep. 36: 80 p.

FEDERAL ENVIRONMETNAL ASSESSMENT REVIEW OFFICE. 1983. CN Rail Twin Tracking Program, British Columbia. Interim Report of the Environmental Assessment Panel. Can. Fed. Environ. Assess. Rev. Process No. 23: 21 p.

GLOVA, G. J. AND J. E. MCINERNY. 1977. Critical swimming speeds of coho salmon (*Oncorhynchus kisutch*) fry to smolt stages in relation to salinity and temperature. J. Fish. Res. Board Can. 34: 151−154.

LISTER, D. B. 1981. CN Twin Tracking Program—Valemont to Vancouver. A synthesis of related fish passage literature. Report prepared for CN Rail. D. B. Lister and Assoc. Ltd., Clearbrook, B.C. 35 p.

MALINUN, L. K. 1973. Speed of fish migration. Fish. Ind. 8: 77−79. (Transl. Ser. No. 2171. J. Fish. Res. Board Can. 1972. 8 p.)

SIMPSON, G. G., A. ROE, AND R. C. LEWONTIN. 1960. Quantitative zoology (revised edition). Harcourt, Brace and World Inc., New York, NY. 440 p.

STASKO, A. B., R. M. HORRALL, A. D. HORBER, AND D. STASKO. 1973. Coastal movements of mature Fraser River pink salmon (*Oncorhynchus gorbuscha*) as revealed by ultrasonic tracking. J. Fish. Res. Board Can. 30: 1309−1316.

WARD, F. J. 1959. Character of the migration of pink salmon to the Fraser River spawning grounds in 1957. Bull. Int. Pac. Salmon Fish. Comm. 10: 70 p.

WEBB, P. W. 1975. Hydrodynamics and energetics of fish propulsion. Bull. Fish. Res. Board Can. 190: 159 p.

WILLIAMS, I. V., J. R. BRETT, G. R. BELL, G. S. TRAXLER, J. BAGSHAW, J. R. MCBRIDE, U. H. M. FAGERLUND, H. M. DYE, J. P. SUMPTER, E. M. DONALDSON, E. BILINSKI, H. TSUYUKI, M. D. PETERS, E. M. CHOROMANSKI, J. H. Y. CHENG, AND W. L. COLERIDGE. 1986. The 1983 early run Fraser and Thompson River pink salmon; morphology, energetics and fish health. Bull. Int. Pac. Salmon Fish. Comm. 23: 55 p.

Food Selection by Yellowtail Flounder (*Limanda ferruginea*) on Georges Bank[1]

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Collie, J. S. 1987. Food selection by yellowtail flounder (*Limanda ferruginea*) on Georges Bank. Can. J. Fish. Aquat. Sci. 44: 357–367.

Yellowtail flounder (*Limanda ferruginea*) stomachs and benthic grab samples were collected concurrently at three sites on four quarterly dates from August 1982 to May 1983. Stomach contents and grab samples were sorted and weighed and important prey species measured. Yellowtail flounder feed mainly on benthic macrofauna; in most cases a few amphipod and polychaete species constituted the bulk of the diet. I calculated selection indices to compare the species and size composition of the stomach contents with that of the benthic macrofauna. The selection indices are consistent among the four sampling dates and can largely be explained by prey life history and prey size. A lognormal curve, fitted by least squares, accounts for 87% of the variation in the mean size-selection indices. According to this curve, the preferred prey size of 3-yr-old yellowtail flounder is 13 mg.

À quatre dates trimestrielles de août 1982 à mai 1983, on a recueilli simultanément des échantillons de limande à queue jaune (*Limanda ferruginea*) et de sédiments benthiques à l'aide d'une benne preneuse. Les contenus stomacaux et les échantillons de sédiments ont été triés et pesés et les proies importantes ont été mesurées. La limande à queue jaune se nourrit surtout de la macrofaune benthique; dans la plupart des cas, quelques espèces d'amphipodes et de polychètes constituaient la majeure partie du régime. L'auteur a calculé des indices de sélection afin de comparer les espèces et la composition par taille des proies retrouvées dans les contenus stomacaux avec celles constituant la macrofaune benthique. Les indices de sélection sont uniformes dans le cas des quatre dates d'échantillonnage; le cycle vital et la taille des proies justifient en grande partie ces indices. Une distribution lognormale, ajustée par la méthode des moindres carrés, permet d'expliquer 87 % de la variation des indices moyens de sélection selon la taille. Selon cette distribution, une limande à queue jaune de 3 ans préfère une proie de 13 mg.

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The yellowtail flounder (*Limanda ferruginea*) is a right-handed, small-mouthed flounder that occurs along the eastern seaboard of North America from Labrador to Chesapeake Bay, usually at depths of 10–100 m (Bigelow and Schroeder 1953). This fish has contributed significantly to the commercial flatfish catch off New England since the 1930s (Clark et al. 1984) and on the Grand Banks since 1965 (Pitt 1970). With a single row of fine teeth and pronounced downward orientation, the yellowtail flounder's small mouth is adapted for benthivory. Previous food-habits studies (Pitt 1976; Libey and Cole 1979; Hacunda 1981; Langton and Bowman 1981; Langton 1983; Bowman and Michaels 1984) confirmed the importance of polychaetes and benthic amphipods in the diet of this fish. In this study I analyzed the food habits of the yellowtail flounder in relation to the abundance and size of benthic prey species.

Selection indices measure the utilization of food types (r) in relation to their abundance or availability in the environment (p). Among the family of mathematically related selection indices, Chesson's (1978) α index is one of the most useful (Lechowicz 1982). This index is calculated as the forage ratio normalized by the sum of all forage ratios:

$$(1)\quad \alpha_j = (r_j/p_j) \Big/ \sum_{m=1}^{n} (r_m/p_m).$$

Subscripts j and m refer to the various prey categories. Alpha varies exponentially from 0 to 1; neutral selection corresponds to $1/n$, where n is the number of prey categories. The advantages of α are that it is insensitive to changes in prey abundance and it is approximately multivariate normally distributed. These properties enabled Schmitt and Holbrook (1984a, 1984b) to use multivariate analysis of variance for comparing size selection between black surfperch (*Embiotica jacksoni*) and striped surfperch (*E. lateralis*) and among different size classes of black surfperch.

Most food-habits studies of marine fish have measured *either* species selection (Frame 1974; Gabriel and Pearcy 1981; Sedberry 1980; MacDonald and Green 1986) *or* size selection (Levings 1974; Schmitt and Holbrook 1984a, 1984b); none have explicitly investigated the interaction between species and size preference. The potential pitfall in these studies is that apparent species selection could be due to prey size; conversely, apparent size selection could be due to prey availability. Unless species *and* size selection are measured, the

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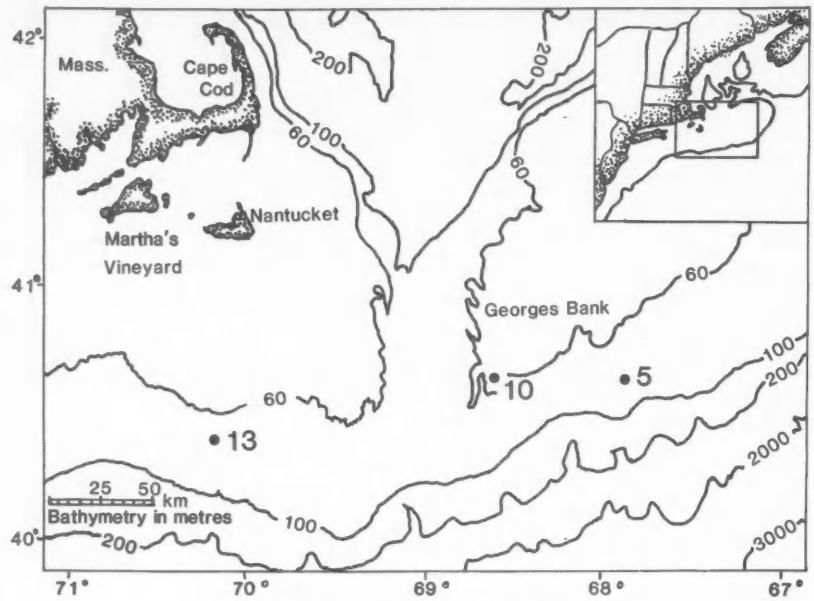

FIG. 1. Sampling locations off the New England coast.

importance of these two factors in prey selection cannot be distinguished.

A mathematical treatment of fish stomach contents, in relation to prey abundance, that accounts for both species (i) and size (j) selection was formulated by Andersen and Ursin (1977) and described in detail by Andersen (1982). Andersen's suitability coefficient (G_{ij}) is the product of a vulnerability coefficient (ρ_i) and a size-preference coefficient (g_{ij}). The vulnerability coefficient (ρ_i) is, by definition, size independent; investigations on cod (*Gadus morhua*) and dab (*Limanda limanda*) (Ursin 1973) suggested that g_{ij} is a lognormal function of the predator-to-prey weight ratio. I show in the methods section of this paper that the suitability coefficient (G_{ij}), when normalized to unity, is exactly equivalent to the α index calculated over prey species and prey size (α_{ij}).

To estimate the parameters of Andersen's model, one requires complete data on the identity and sizes of prey in the predator's diet and in the environment. Because of these data requirements, in only a few cases has the model been applied to field data (Arntz and Ursin 1981; Dekker 1983; Ursin and Arntz 1985a, 1985b, 1985c). These five studies showed that, in some cases, size selection (g) is a lognormal function of prey weight, but they suffered a number of common deficiencies. The main problem was estimating the abundance and size of available prey. For fish as prey, abundance was basically unknown and the size spectrum was assumed to be either constant over logarithmic size classes (Dekker 1983) or some function of prey size (Ursin and Arntz 1985a, 1985b, 1985c). In only one case (Arntz and Ursin 1981) were the vulnerability coefficients (ρ_i) estimated. In all cases, only the mean size of each prey species was measured; the actual size–frequency distributions were unknown. Finally, in all cases except Dekker (1983), the authors pooled data from all seasons, thus ignoring seasonal changes in prey size distributions.

In my study, data were collected with the aim of fitting the parameters of Andersen's model. Yellowtail flounder are primarily benthivores, so a high degree of overlap exists between stomach contents and benthic grab samples. The number and weight of each prey species were measured in both sample types. In addition, individual size distributions of important prey species were measured. The analysis explicitly accounts for both species and size selection; in other words, it compares selection for prey species i, size j against prey species k, size m. By sampling four times during 1 yr, I could test whether the suitability coefficients (G_{ij}) remained constant as the prey size distributions varied seasonally.

Materials and Methods

Fish stomachs were collected on a quarterly basis from August 1982 to May 1983 on cruises conducted by the Northeast Fisheries Center (National Marine Fisheries Service, Woods Hole, MA). Stomach collection coincided as closely as possible to the dates and locations of benthic sampling conducted as part of the Georges Bank Benthic Infauna Monitoring Program (Battelle and Woods Hole Oceanographic Institution 1985). I chose monitoring Stations 5, 10, and 13 (Fig. 1) for fish stomach analysis because the macrofaunal assemblages differ significantly among these sites. Stations 5 and 10 are located on the southern flank of Georges Bank at 84 and 60 m depth, respectively (Fig. 1). Station 13, at 69 m depth, is located in the area south of Nantucket known locally as the "mudpatch." At each site, trawling was conducted within a 5-km square centered at the station coordinates.

A No. 35 otter trawl, towed at 3-h intervals, usually over a 24-h period at each station, collected the fish samples. Tow duration was generally 30 min at 5.5–6.5 km·hr^{-1}. Fish stomachs were excised at sea, preserved in 10% formalin in seawater, and labelled. At the Battelle Laboratory (397 Washington Street, Duxbury, MA) each stomach was cut longi-

tudinally and the entire bolus removed and wet-weighed to the nearest 1 mg after blotting. Stomach contents were sorted to species and enumerated. Fragments were counted if the head was present and an indentification could be made. The taxonomic characters needed to identify the two species of *Unciola* include the third epimeral plate and fifth coxa. The 17% of *Unciola* lacking these characters could not be sorted to species and were recorded as *Unciola* spp. These individuals were assigned to *U. inermis* and *U. irrorata* according to the relative proportions of identifiable individuals of the two species for that station and date. Individuals of each species were weighed together to the nearest 1 mg.

At each station, on each benthic sampling cruise, six replicate, 0.04-m^2, modified van Veen grab samples were collected, sieved on a 0.3-mm screen, and preserved in 10% formalin. Workers at the Battelle Laboratory resieved each sample and then sorted, enumerated, and identified to species the organisms recovered. Individuals of each species were weighed together to the nearest 1 mg. The benthic communities at these sites are fully described in the Benthic Monitoring Program Final Report (Battelle and Woods Hole Oceanographic Institution 1985).

Size–frequency measurements were made of six prey species that were numerous in yellowtail flounder stomachs and benthic grab samples: *U. inermis* and *Ericthonius fasciatus* from stomachs collected at Station 5, *Echinarachnius parma* from stomachs at Station 10, and *Ampelisca agassizi*, *Chone infundibuliformis*, and *Levinsenia gracilis* at Station 13. Sample sizes permitting, length–frequency distributions of the three amphipod species were based on at least 200 individuals. I subsampled, with a plankton splitter, stomachs containing large numbers of amphipods such that about 200 prey of each species were measured from each season.

Size–frequency distributions of the other three species were based on 100 measurements because these species were less numerous. Total length was the measurement used for all species except *L. gracilis*, for which setiger number was used instead. I determined wet weight – length relationships for each prey species using live animals collected in May 1983.

I calculated food selection indices to compare the species composition of the stomach contents with that of the benthic macrofauna and to estimate the parameters of Andersen's (1982) feeding model. Andersen's model is based on the assumption that the weight of prey species i, size class j in the diet (S_{ij}), relative to the entire stomach contents (S), is proportional to its availability (ϕ_{ij}) relative to the total availabe food (ϕ):

$$(2)\quad S_{ij}/S = \phi_{ij}/\phi.$$

Although stomach contents data may be biased by differential prey digestion rates, in the absence of prey-specific digestion rates I assumed that the stomach contents accurately reflected the diet.

Available food (ϕ_{ij}) is defined as biomass (B_{ij}) weighted by the suitability coefficient (G_{ij}):

$$(3)\quad \phi_{ij} = B_{ij}G_{ij}.$$

Substituting Eq. 3 into Eq. 2:

$$(4)\quad S_{ij}/S = B_{ij}\,G_{ij}\Big/\sum_{km}\sum(B_{km}G_{km})$$

where subscript k indicates prey species and m indicates size class. Multiplication of all G terms by the same constant would not change Eq. 4. Thus, without changing the biological properties of G, I can add the constraint

$$(5)\quad \sum_k\sum_m G_{km} = 1.0.$$

Solving for G_{ij} in Eq. 4, and using the identity in Eq. 5, Beyer and Sparre (1983) obtained

$$(6)\quad G_{ij} = (S_{ij}/B_{ij})\Big/\sum_k\sum_m(S_{km}/B_{km}).$$

If prey are classified by species and size, in the diet and in the environment, an array of G_{ij} values can be calculated.

In electivity notation:

$$(7a)\quad r_{ij} = S_{ij}\Big/\sum_k\sum_m S_{km}$$

and

$$(7b)\quad p_{ij} = B_{ij}\Big/\sum_k\sum_m B_{km}.$$

By substituting these equalities back into Eq. 6,

$$(8)\quad G_{ij} = (r_{ij}/p_{ij})\Big/\sum_k\sum_m(r_{km}/p_{km}) = \alpha_{ij},$$

it is easily shown that G_{ij} is exactly equivalent to Chesson's (1978) α. This two-dimensional selection index is flexible in that it can accommodate a situation in which not all prey species were measured, or conversely, it can accommodate a situation in which some taxa were measured but not identified.

The suitability coefficient (G_{ij}) is the product of a vulnerability coefficient (ρ_i) and a size-preference coefficient (g_{ij}):

$$(9)\quad G_{ij} = \rho_i\, g_{ij}.$$

The size-preference coefficient (g_{ij}) is assumed to be a log-normal function of the predator-to-prey weight ratio (W/w) such that

$$(10)\quad G_{ij} = \rho_i \exp\left[-(\log(W/w_j) - \eta_i)^2/2\sigma_i^2\right]$$

where η_i is the logarithm of the preferred or optimal predator-to-prey weight ratio, and the standard deviation, σ_i, measures the breadth of size selection. Taking logarithms of Eq. 10,

$$(11)\quad \log G_{ij} = \log \rho_i - (\log(W/w_j) - \eta_i)^2/2\sigma_i^2$$

gives a quadratic function of $\log(W/w_j)$ that can be fit by least squares to the observed series of G_{ij} values.

The suitability coefficient was originally formulated (Andersen and Ursin 1977) on the basis of prey weights rather than prey numbers, but provided the prey are counted and

TABLE 1. Relationships between length (L) (mm) and wet weight (W) (mg) for five species as fitted by linear regression to the equation $\log(W) = a + b\log(L)$. All weights are from live animals except for *C. infundibuliformis* in which case only preserved worms were available.

Species	n	a	b	r^2
Ampelisca agassizi	87	0.020	2.70	0.97
Unciola inermis	39	0.050	2.48	0.97
Ericthonius fasciatus	86	0.025	2.48	0.98
Chone infundibuliformis	48	0.019	2.59	0.87
Echinarachnius parma	66	0.839	2.38	0.97

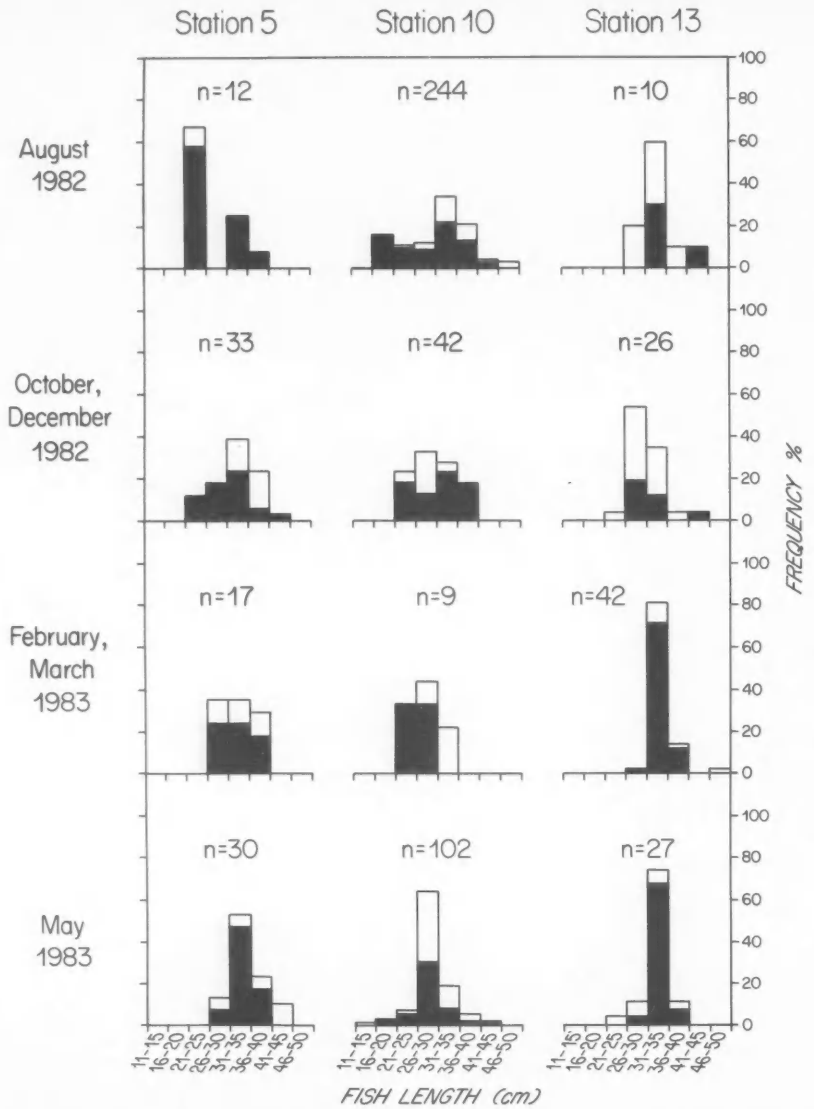

FIG. 2. Length distributions of yellowtail flounder collected for stomach analysis. Solid bars represent stomachs containing recognizable food; open bars represent stomachs with no recognizable food.

weighed accurately, it is easily shown that G values are identical whether calculated with weights or numbers. In this study I used prey numbers rather than weights because ingested prey weights are biased by partial digestion and because, in some benthic samples, the biomass is dominated by a few large animals with hard skeletons such as *Arctica islandica* and *E. parma*.

For those prey species not measured, I have only the numbers in the diet, S_i, and in the benthos, B_i. I calculated S_i and B_i by summing over all fish stomachs and all benthic replicates from a given station and date, respectively. Size–frequency distributions cannot be calculated for individual fish stomachs because each stomach did not contain enough prey to construct a representative distribution. For similar reasons, size–frequency distributions were not obtained for each benthic replicate, but I assumed that the distributions I did obtain represent each replicate in the sample (Collie 1985b, chap. 1).

For those species that were measured, I used the length–frequency distributions (e.g. Fig. 4) to partition S_i and B_i into size classes. The size–frequency distributions measured from stomach contents should not be biased by partial digestion because they are based on length measurements that are exactly equivalent for ingested and noningested prey. I converted the length classes (Fig. 4) to weight classes using the appropriate length–weight regression (Table 1). I fit Eq. 11 by least squares to the array of α_{ij} values calculated using Eq. 8.

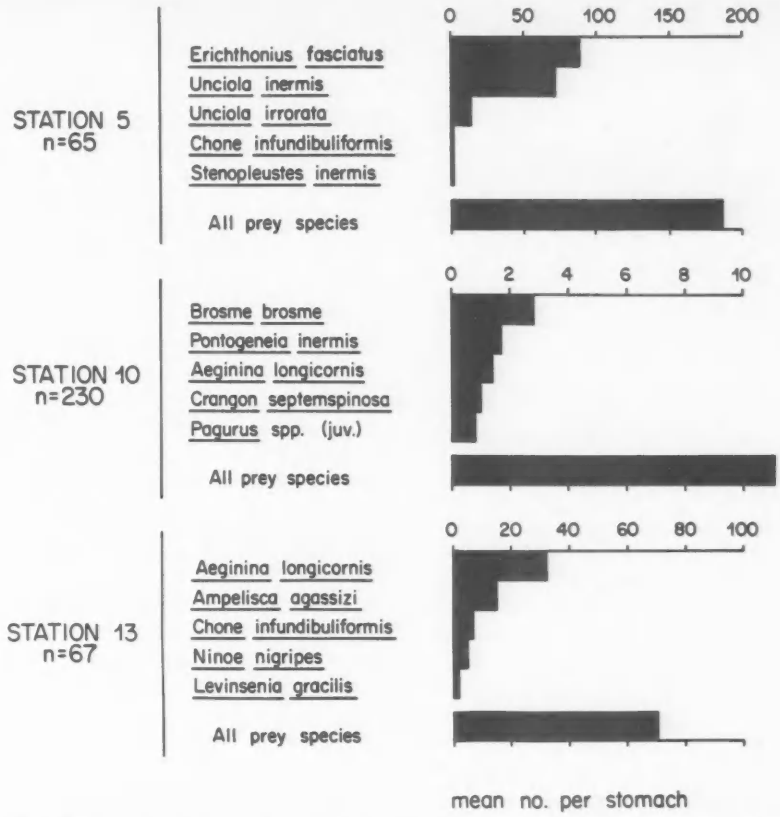

FIG. 3. Five most numerous prey species of yellowtail flounder at Stations 5, 10, and 13. Data are weighted means of all stomachs collected on four quarterly cruises.

Results

A total of 594 yellowtail flounder stomachs were examined; 400 of these contained recognizable food; 194 did not. Most of the yellowtail flounder were between 26 and 35 cm long (Fig. 2), corresponding to an age of 3 yr (Lux and Livingston 1982). Because of the small sample sizes and because most of the flounder occurred in only two of the size classes, I was unable to examine the potential effect of predator length on diet composition.

At each station and date, a few prey species constituted the bulk of the yellowtail flounder diet. The five most numerous prey species at each station (Fig. 3) accounted for 96, 70, and 89% of the total identifiable prey at Stations 5, 10, and 13, respectively. The stomach contents of these fish are tabulated, by numbers and by weight, in Collie (1985b, appendix B).

At Station 5 the diet was dominated by tubicolous amphipods and polychaetes. *Lumbrineris fragilis* was important on a weight basis although only eight of these large worms were eaten. Of 64 prey species, 52 were also collected in benthic grab samples, 3 were pelagic, and 9 were not found in the grab samples even though they are benthic animals. The 12 species not found in grab samples constituted an insignificant proportion of the total diet. Pelagic prey were more important at Station 10 where the diet was dominated by fish larvae, amphipods, shrimps, and crabs. Large benthic animals, such as *Cerianthus borealis*, *E. parma*, and *L. fragilis*, constituted much of the stomach content weight. Of 50 prey species at Station 10, 31 were also collected in benthic grab samples and 4 were pelagic. Of the 19 species not found in grab samples, 9 were important components of the flounder diet. At Station 13 the diet was dominated by amphipods numerically and by polychaetes on a weight basis. Of 56 prey species, 47 were also collected in benthic grabs and 2 were pelagic. None of the nine species not found in grab samples were important dietary components.

Fish caught at Station 5 had the highest mean number of prey per stomach, followed in turn by those caught at Stations 13 and 10. Because the mean weight of stomach contents was only slightly greater at Station 5 (707 mg) than at Station 13 (680 mg) and Station 10 (528 mg), most of the differences in prey number are due to differences in mean prey weight. On the average, flounder ate larger prey at Station 10 (54 mg) than at Station 13 (10 mg) or Station 5 (4 mg).

At Station 5 the same prey species dominated the diet at all seasons (Battelle and Woods Hole Oceanographic Institution 1984, fig. 69). In contrast, there was considerable seasonal variation in the diet at Station 10, where the diet was dominated by larvae of cusk (*Brosme brosme*) in August, by the shrimp *Crangon septemspinosa* in the fall and winter, and by the

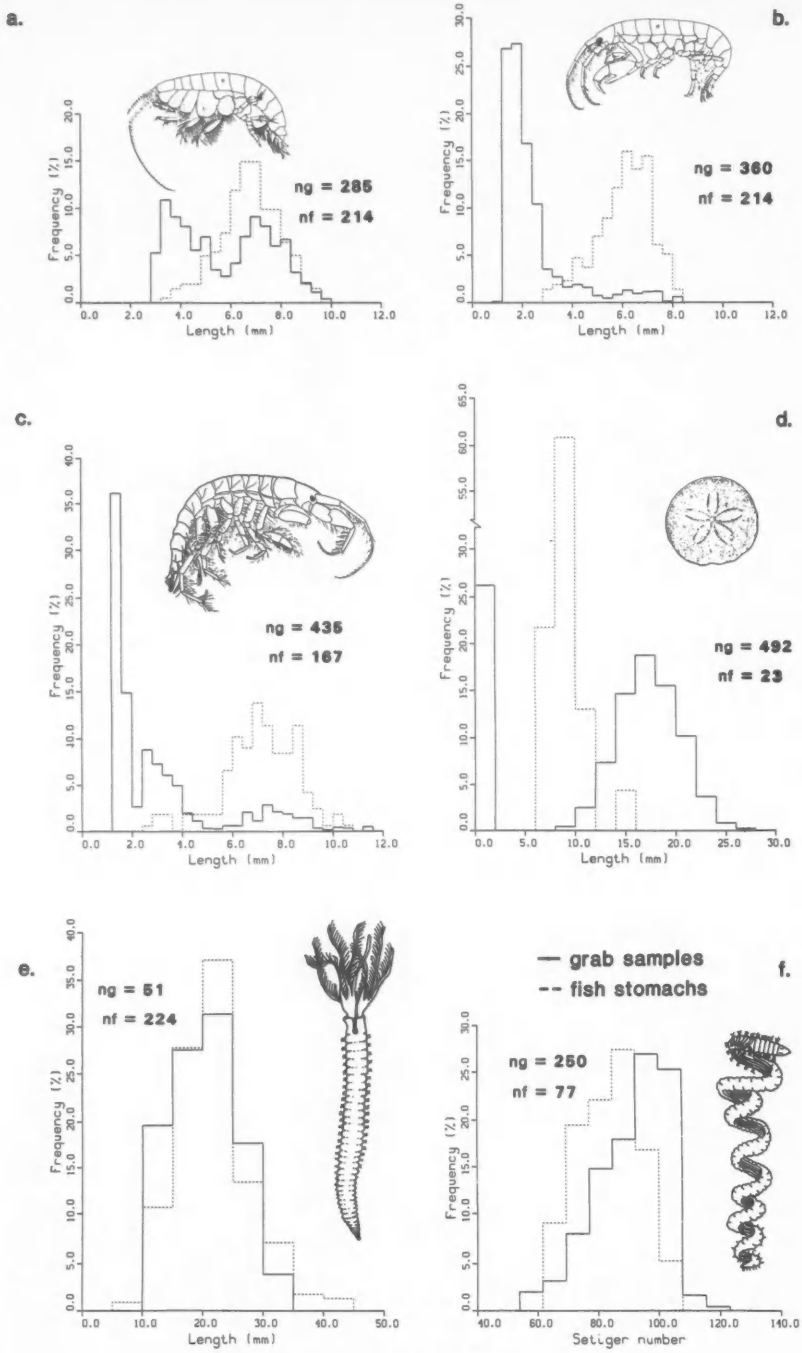

FIG. 4. Size–frequency distributions of available (solid line) and ingested (broken line) prey. The symbols *ng* and *nf* indicate the number of animals measured from the grab samples and fish stomachs, respectively. (a) *Ampelisca agassizi* at Station 13 in May 1983; (b) *E. fasciatus* at Station 5 in May 1983; (c) *U. inermis* at Station 5 in May 1983; (d) *E. parma* at Station 10 from July 1982 to May 1983; (e) *C. infundibuliformis* at Station 13 from July 1982 to May 1983; (f) *L. gracilis* at Station 13 from February to May 1983.

amphipods *Pontogeneia inermis* and *Aeginina longicornis* in May. At Station 13 the diet was relatively constant except for the epifaunal caprellid *A. longicornis*, which was eaten in great numbers in winter but much less at other times of the year.

Examples of the size–frequency distributions generated from the fish stomach contents and from benthic grab samples are compared in Fig. 4, with all frequencies expressed as percentages. Due to small numbers of individuals collected, it was not possible to generate size–frequency distributions for all four seasons for all six prey species measured; in some cases it was necessary to pool size data from more than one season.

In general, yellowtail flounder neglected the small 2- to 5-mm amphipods (Fig. 4a, 4b, 4c), selecting the 5- to 8-mm size range. The same size-selection pattern was evident in all four seasons, but it was particularly apparent in May 1983, which was a period of recruitment for both *U. inermis* and *E. fasciatus*. Yellowtail flounder ate only the intermediate sizes of the sand dollar *E. parma* (Fig. 4d), even though these sizes were rare or absent in the benthos. For the polychaete *C. infundibuliformis*, the fish stomach and grab sample length–frequency distributions are very similar (Fig. 4e). Flounder fed on the same size range of *L. gracilis* as occurred in the benthos (Fig. 4f), but because the fish stomach size–frequency distribution is more normally distributed, it appears that the fish selected smaller-sized worms.

I calculated α selection indices to determine whether changes in prey composition reflect seasonal changes in benthic community composition. Constant α for a given prey species indicates that fish feeding mirrors changes in prey abundance. Variations in α are due to prey suitability changing during the year and/or sampling error.

Initially I calculated α_i on the basis of prey species only, disregarding the size–frequency data, in order to compare selectivity among those prey species not measured. The α value corresponding to neutral selection is $1/n$, where n is the number of prey species. I took n to be the number of species found both in the fish stomachs and in the grab samples during at least one season. This gives a slightly higher neutral value than if n were the total number of species in the benthic grab samples. Some benthic species are not suitable prey for yellowtail flounder because they are too small or burrow too deeply. The neutral value is the same for all species and seasons at a given station but varies slightly among stations because the numbers of prey species are different. When examining Fig. 5, one must remember that α is based on proportions, and the sum of α for each season is unity. Therefore, an increase in α for one species results in a decrease for other species and it is impossible to determine causality from the index alone.

Of the three stations, seasonal α values were most consistent at Station 5 (Fig. 5a), owing to the high degree of overlap between the contents of the fish stomachs and grab samples there. Alpha values were least consistent at Station 10 (not shown), due to the predominance in the diet of pelagic species and benthic species not found in grab samples. Seasonal α values were more consistent at Station 13 (Fig. 5b) except in February when *A. longicornis* dominated the diet but remained rare in the grab samples. The high α value for *A. longicornis* is matched by correspondingly low values for the remaining species.

The yellowtail flounder diet is plastic in that the dominant species vary from station to station. On the other hand, α values are consistent for those prey species eaten at two or more stations. For example, *A. longicornis* was positively selected at all three stations. *E. fasciatus* was almost neutrally selected at Station 5 and slightly negatively selected at Station 13. *Chone infundibuliformis* was positively selected at Stations 5 and 13; *C. duneri* was neutral to slightly negatively selected at the same stations. Finally, *L. fragilis* was neutrally selected at Station 10 and slightly positively selected at Station 5.

Figure 6 is a composite of α_{ij} values of five prey species plotted against prey weight on log–log axes. The *E. fasciatus* and *U. inermis* data are from Station 5, the *E. parma* data from Station 10, and the *A. agassizi* and *C. infundibuliformis* data from Station 13. Since selectivity values are consistent among stations, as explained above, this among-station comparison of α_{ij} should be valid. For most prey size classes, I could calculate α_{ij} values for all four seasons. For the purpose of calculating $1/n$ (the value corresponding to neutral selection), n is now the total number of prey categories (species plus size). Together, the five prey species describe a composite, dome-shaped, size-selection curve and define the upper and lower size limits of food acceptable to yellowtail flounder. Prey items between about 2 and 200 mg are positively selected by yellowtail flounder.

Size selection for the three amphipod species (open symbols) was strongly negative for the smallest (juvenile) size classes and increased with prey size. All sizes of the polychaete *C. infundibuliformis* were positively and more or less equally selected. I calculated α_{ij} values for the *L. gracilis* size classes shown in Fig. 4f, but, lacking a conversion from setiger number to wet weight, I could not plot this species' α_{ij} values in Fig. 6. All size classes of *L. gracilis* were negatively selected, as would be expected for such a small worm (mean weight 0.3 mg).

Only three of the *E. parma* size classes (Fig. 4d) appeared both in the fish stomachs and grab samples; selectivity for these three decreased with prey size. Juvenile sand dollars, weighing approximately 0.5 mg each, were numerous in the grab samples but never eaten by flounder. Intermediate-sized sand dollars, weighing about 40 mg each, were eaten but did not appear in the grab samples. Sand dollars larger than 500 mg each, although abundant at Station 10, were not eaten by flounder. *Echinarachnius parma*, by itself, probably describes a dome-shaped size-selection curve but, unfortunately, only three of these sizes can be plotted in Fig. 6.

In fitting the size-selection function (Eq. 11) to the observed α_{ij} values, I was unable to fit a separate curve for each prey species because each one covers only part of the size range. Therefore, I assumed that the five prey species share the same size-selection parameters (η_i and σ_i) but have different vulnerability coefficients (ρ_i). The vulnerability coefficient (ρ_i) determines the relative vertical displacement of the size-selection curves; fitting a separate ρ_i for each species tends to draw the α_{ij} values in Fig. 6 onto the same curve. Because multiplication of all G (or α) terms by the same constant does not change their relative values, the values of ρ_i cannot be determined uniquely but only in relation to one another. The estimated vulnerability coefficients, relative to 1.0 for *U. inermis*, are 0.21 for *A. agassizi*, 2.69 for *E. fasciatus*, 10.18 for *C. infundibuliformis*, and 1.34 for *E. parma*. The significance of these ρ_i values is that they measure the suitability of a prey species independently of its size.

I fit Eq. 11 by least squares to the mean α_{ij} values; thus the r^2 of 0.87 does not account for among-season variation as indicated by the vertical lines in Fig. 6. The dotted curve in Fig. 6 (a lognormal curve is parabolic when plotted on log–log

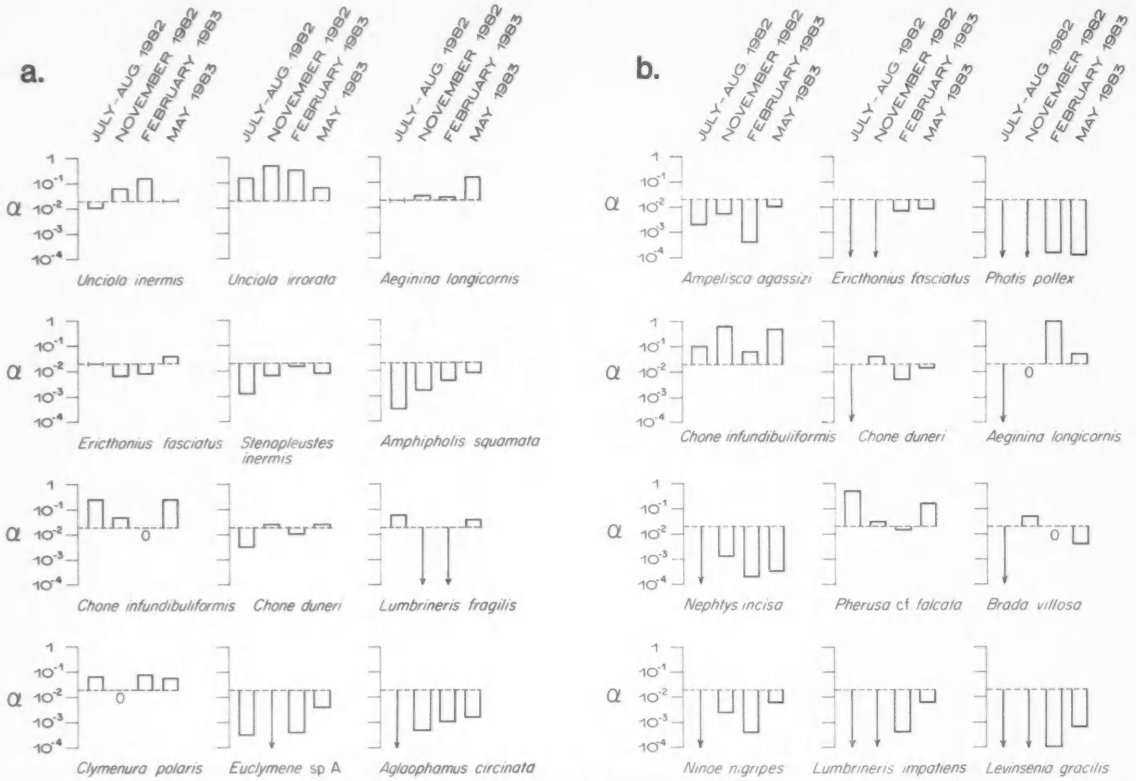

FIG. 5. Yellowtail founder selectivity for benthic prey at (a) Station 5 and (b) Station 13. The broken line in each subplot is the value for neutral selection. Arrows indicate that the prey species was present in benthic grab samples but not eaten by flounder on that date; α is zero in this case. Zeros below the broken lines indicate that the prey species was not found in benthic grab samples on that date; in this case α is undefined.

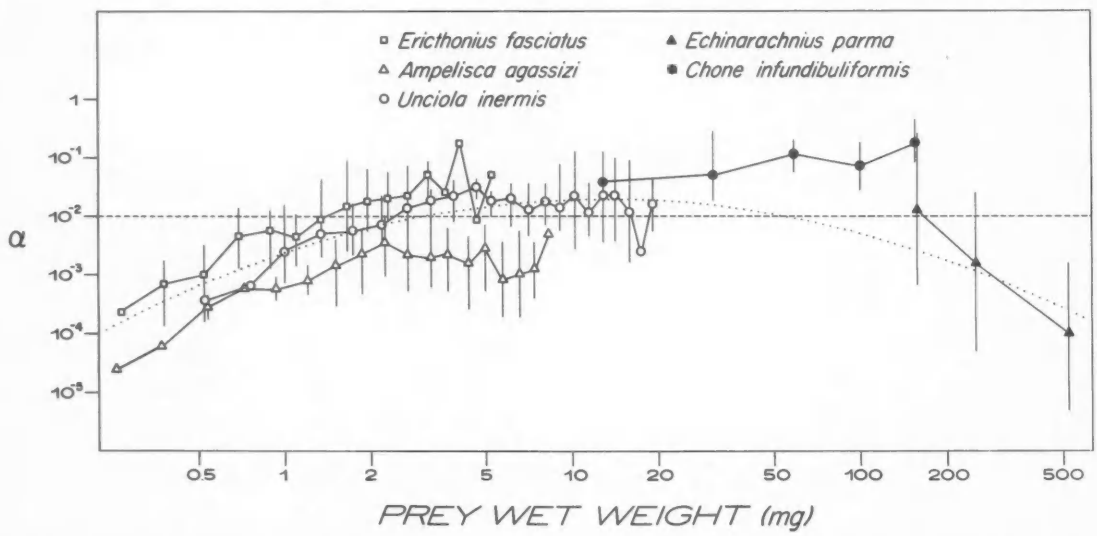

FIG. 6. Yellowtail flounder size selectivity for five benthic prey species. The symbols indicate the means of four seasonal values and the vertical lines indicate the ranges between minimum and maximum α values. The broken line is the value for neutral selection. The dotted line is the least squares fit of Eq. 11.

axes) corresponds to $\rho_i = 1.0$ for *U. inermis*; size-selection curves for the other prey species would be shifted up or down according to the ρ_i values listed above. Size selection alone accounts for 53% of the variation in mean α_{ij} values; the ρ_i parameters account for a further 34% of the variation. According to this fit, the preferred prey weight is 13.3 mg and the standard deviation (σ) of the lognormal size-selection function is 0.55 log (mg).

Discussion

Many of the important prey species in this study are the same as those found in previous food habits studies (e.g. Hacunda 1981; Langton 1983; Bowman and Michaels 1984). These species include polychaetes (*Lumbrineris* spp. and *Nephtys* spp.), amphipods (*Unciola* spp.), and decapods (*C. septemspinosa*). Yellowtail founder feed mainly during the daylight hours (Langton 1983; Collie 1985b) and prey (probably visually) on animals living on or near the sediment surface. The selection indices in Fig. 5 can be interpreted in relation to where the prey species live, how they feed, and what size they are. Prey sizes, given in parentheses in the following paragraphs, are mean weights from all fish stomachs at each station and were calculated by dividing the total weight of each species by the number of individuals. Although biased by partial digestion, these weights provide relative sizes for those species not individually measured.

The numerically dominant prey species at Station 5, *E. fasciatus* and *U. inermis*, are both tubicolous amphipods and were approximately neutrally selected (Fig. 5a). Although much less abundant than *U. inermis* in the benthos, *U. irrorata* was more strongly selected for by yellowtail flounder. Usually, *U. irrorata* inhabits tubes constructed by other amphipods or polychaetes, but can build a tube of its own if no others are available (Bousfield 1973). Smith (1950) observed these amphipods swimming or roaming across the bottom, leaving their tubes for considerable lengths of time. *Unciola irrorata* (4.5 mg) is more strongly selected than *U. inermis* (3.3 mg), perhaps because it is more epifaunal in habit or because it is larger.

The caprellid amphipod *A. longicornis* (3.2 mg) has been collected from sea grass, macroalgae, hydroids, and bryozoans (McCain 1968); this epibenthic habit explains its positive selectivity by flounder. The amphipod *Stenopleustes inermis* is also thought to live on hydroids because other species in its genus have been collected from hydroids (Lincoln 1979) and alcyonarians (Sars 1895). *Stenopleustes inermis* is not as strongly selected for by yellowtail flounder as are the other amphipod species, perhaps because of its smaller size (1.7 mg). The brittle star, *Amphipholis squamata* (2.7 mg), burrows superficially in sandy substrata (Gosner 1971) and may thereby avoid predation.

The sabellid polychaetes *C. infundibuliformis* and *C. duneri* feed with tentacles above the surface (Fauchald and Jumars 1979), exposing themselves to predation. *Chone infundibuliformis* (31.8 mg) was selected more strongly than the smaller species, *C. duneri* (6.5 mg). Most lumbrinerid polychaetes are burrowers (Fauchald and Jumars 1979), which makes them less vulnerable to predation by flounders. *Lumbrineris fragilis* was positively selected by flounder probably because of its large size (851.0 mg). Most maldanids are tubicolous (Fauchald and Jumars 1979); of the two maldanids included in Fig. 5a, the larger, *Clymenura polaris* (19.5 mg), was selected for and the smaller, *Euclymene* sp. A (3.3 mg), was selected against. All nephtyids are free-living burrowers (Fauchald and Jumars 1979); this probably explains why *Aglaophamus circinata* was negatively selected despite its large size (51.4 mg).

Station 13 (Fig. 5b) had the greatest overlap between fish diet and macrobenthos. *Ampelisca agassizi*, the dominant amphipod species there, builds its tubes vertically into the substratum and may thus avoid predation. Another amphipod species, *Photis pollex*, was strongly selected against, probably because of its small size (0.3 mg). The flabellegerid polychaetes *Pherusa* cf. *falcata* (108.9 mg) and *Brada villosa* (51.2 mg) are surface-dwelling deposit-feeders (Fauchald and Jumars 1979); together with their large size, this probably explains their positive selection by flounder. The remaining polychaete species are all subsurface burrowers and were all negatively selected.

The minimum suitable prey size, as indicated by selection against juvenile amphipods and sand dollars, could be defined by two factors. A sensory limit may exist if flounder cannot detect prey below a certain size. Or, foraging for such small prey may be energetically inefficient. The maximum suitable prey size is defined by the absence of large sand dollars in the diet despite their abundance in the benthos. Since sand dollars are hard and approximately round, the width of a sand dollar must pass through the flounder mouth. Judging from gape measurements of yellowtail flounder (Hacunda 1981), a 16-mm sand dollar is about the largest that could fit through the mouth of a 30-cm flounder.

Based on investigations of the prey size preferences of cod and dab (Ursin 1973), Andersen and Ursin (1977) proposed that size selection is a lognormal function of prey size (Eq. 10). According to this hypothesis, a prey item twice as large as the optimum size should be selected equally to a prey item one half the optimum size. In contrast, Zaret (1980) argued that gape-limited predators should prefer the maximum prey size they can swallow, such that the pattern of selectivity should abruptly truncate at the maximum prey size set by morphology. Schmitt and Holbrook (1984b), testing this hypothesis, found that black surfperch and striped surfperch were not gape limited and that size-selection curves were roughly bell shaped. In my study, α falls off abruptly for large *E. parma*, suggesting a truncated distribution, but the α values have too much scatter to draw a firm conclusion. The upper size limit imposed by gape limitation is certainly more rigid than the lower, more flexible size limit imposed by foraging constraints.

In only a few cases have the size-selection parameters of Andersen's model been estimated. Arntz and Ursin (1981) calculated an array of η values for various size classes of dab (*L. limanda*) feeding on nine prey species; the mean η of value was 3.6 ($\log_{10}$). Hahm and Langton (1984) calculated frequency distributions of predator-to-prey weight ratios (W/w) for 11 northwest Atlantic fishes including yellowtail flounder. These frequency distributions summarize the observed weight ratios, not the preferred weight ratios, because the distribution of available prey sizes is unknown. Observed weight ratios, log (W/w), would equal preferred weight ratios (η) only if prey abundance were uniform over logarithmic size classes. The frequency distributions of W/w are approximately lognormal; for flounder the mean and standard deviation of the distribution were 4.2 and 0.87 ($\log_{10}$).

My composite size-selection curve (Fig. 6) was fit reasonably well by a lognormal curve (dotted line). The overall mean weight of yellowtail flounder caught in this study was 312 g

(Collie 1985b) and the preferred prey size was 13 mg. Thus, the predator-to-prey weight ratio is about 24 000:1 ($\eta = 4.4$) and the standard deviation is 0.55. The η estimate is very close to Hahm and Langton's (1984) mean log (W/w) but my standard deviation is less than theirs, which suggests that yellowtail flounder prefer a narrower range of prey sizes than is found in their stomachs.

Even when the suitability coefficients are standardized for the effect of prey size, among-species differences persist, which are quantified by the vulnerability coefficients (ρ_i). Among the amphipod species, *E. fascictus* is most strongly selected and *A. agassizi* the least selected. The most epifaunal in habit, *E. fasciatus* is most vulnerable to predation, while *A. agassizi*, the most sedentary, avoids predation by building its tubes into the substratum; *U. inermis* is intermediate in these traits (Collie 1985a). Even when the effect of size is removed, *C. infundibuliformis* is preferred over the other prey species considered. As a species, *E. parma* is preferred by flounder but only the intermediate size classes are acceptable. Predation by yellowtail flounder and other fish on the intermediate sizes of *E. parma* could explain the absence of such sand dollars in benthic grab samples and why juvenile *E. parma* did not appear to survive and grow (Battelle and Woods Hole Oceanographic Institution 1985).

Andersen's (1982) interpretation of stomach contents is a useful model for predicting predation patterns provided that the preference parameters are estimated from field data. Most of the among-species differences in selectivity (Fig. 5) can be explained by prey life history and size. Although the least squares fit of Eq. 11 accounted for 87% of the variation in mean α values, there was considerable among-season variation in α not attributable to size. Some of this residual variation is due to the fact that the benthic grab did not adequately sample all the species in the fish diet. This was especially true at Station 10 where the main prey species were pelagic or otherwise rare in benthic grab samples. At Station 13 in February, the high α for *A. longicornis* seems to have depressed α for the remaining species. Residing on hydroids, *A. longicornis* is very patchily distributed and therefore its abundance is not measured well by a small grab sample.

An alternative explanation is that flounder feeding behavior switches in relation to prey abundance. Selection indices assume that prey species are eaten in proportion to their abundance in the environment. However, switching behavior has been observed in several fish species and it is evidently induced by threshold prey densities (Murdoch et al. 1975; Love and Ebeling 1978). My results do not indicate that yellowtail flounder switch prey in relation to prey abundance, but my field study was not designed to detect this more complex behavior; a controlled, manipulative experiment would be required to test this hypothesis.

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References

ANDERSEN, K. P. 1982. An interpretation of the stomach contents of fish in relation to prey abundance. Dana 2: 1–50.

ANDERSEN, K. P., AND E. URSIN. 1977. A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorous circulation and primary production. Medd. Dan. Fisk. Havunders. N.S. 7: 319–435.

ARNTZ, W. E., AND E. URSIN. 1981. Estimates of food consumption parameters for dab *Limanda limanda* utilizing information on food concentrations. An application of Andersen's stomach analysis model. Int. Counc. Explor. Sea C.M. 1981/L:41: 6 p.

BATTELLE AND WOODS HOLE OCEANOGRAPHIC INSTITUTION. 1984. Georges Bank benthic infauna monitoring program: Final report, year two. U.S. Department of the Interior, Minerals Management Service, Washington DC. 173 p.

1985. Georges Bank benthic infauna monitoring program, Vol. 2: Final report, year three. U.S. Department of the Interior, Minerals Management Service, Washington, DC. 333 p.

BEYER, J., AND P. SPARRE. 1983. Modelling exploited fish stocks, p. 485–582. *In* S. E. Jorgensen [ed.] Application of ecological modelling in environmental management. Developments in Environmental Modelling Ser. Vol. 4A. Elsevier, Amsterdam.

BIGEWLOW, H. B., AND W. C. SCHROEDER. 1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv. Fish. Bull. 53: 577 p.

BOUSFIELD, E. L. 1973. Shallow water gammaridean Amphipoda of New England. Cornell University Press, Ithaca, NY. 312 p.

BOWMAN, R. E., AND W. L. MICHAELS. 1984. Food of seventeen species of northwest Atlantic fish. NOAA Tech. Mem. NMFS-F/NEC-28: 183 p.

CHESSON, J. 1978. Measuring preference in selective predation. Ecology 59: 211–215.

CLARK, S. H., M. M. MCBRIDE, AND B. WELLS. 1984. Yellowtail flounder assessment update — 1984. Natl. Mar. Fish. Serv. Woods Hole Lab. Ref. Doc. No. 84-39: 30 p.

COLLIE, J. S. 1985a. Life history and production of three amphipod species on Georges Bank. Mar. Ecol. Prog. Ser. 22: 229–238.

1985b. Feeding habits of the yellowtail flounder and production of its invertebrate prey on Georges Bank. Ph.D. thesis, MIT/WHOI, WHOI-85-32: 165 p.

DEKKER, W. 1983. An application of the Andersen consumption model in estimating prey size preference in North Sea cod. Int. Counc. Explor. Sea C.M. 1983/G:63: 9 p.

FAUCHALD, K., AND P. JUMARS. 1979. The diet of worms: a study of polychaete feeding guilds. Oceanogr. Mar. Biol. Annu. Rev. 17: 193–284.

FRAME, D. W. 1974. Feeding habits of young winter flounder (*Pseudopleuronectes americanus*): prey availability and diversity. Trans. Am. Fish. Soc. 103: 261–269.

GABRIEL, W. L., AND W. G. PEARCY. 1981. Feeding selectivity of Dover sole, *Microstomus pacificus*, off Oregon. Fish. Bull. U.S. 79: 749–763.

GOSNER, K. L. 1971. Guide to indentification of marine and estuarine invertebrates. Wiley-Interscience, New York, NY. 693 p.

HACUNDA, J. S. 1981. Trophic relationships among demersal fishes in a coastal area of the Gulf of Maine. Fish. Bull. U.S. 79: 775–788.

HAHM, W., AND R. LANGTON. 1984. Prey selection based on predator/prey weight ratios for some northwest Atlantic fish. Mar. Ecol. Prog. Ser. 19: 1–5.

LANGTON, R. W. 1983. Food habits of yellowtail flounder, *Limanda ferruginea* (Storer), from off the northeastern United States. Fish. Bull. U.S. 81: 15–22.

LANGTON, R. W., AND R. E. BOWMAN. 1981. Food of eight northwestern Atlantic pleuronectiform fishes. NOAA Tech. Rep. NMFS SSRF-749: 16 p.

LECHOWICZ, M. J. 1982. The sampling characteristics of electivity indices. Oecologia 52: 22–30.

LEVINGS, C. D. 1974. Seasonal changes in feeding and particle selection by winter flounder. Trans. Am. Fish. Soc. 103: 828–832.

LIBEY, G. S., AND C. F. COLE. 1979. Food habits of yellowtail flounder, *Limanda ferruginea* (Storer). J. Fish Biol. 15: 371–374.

LINCOLN, R. J. 1979. British marine Amphipoda: Gammaridea. British Museum (Natural History), London.

LOVE, M. S., AND A. W. EBELING. 1978. Food and habitat of three switch-feeding fishes in the kelp forests off Santa Barbara, California. Fish. Bull.

U.S. 76: 257–271.

LUX, F. E., AND R. LIVINGSTON, JR. 1982. Yellowtail flounder *Limanda ferruginea*, p. 117–119. *In* M. D. Grosslein and T. R. Azarovitz [ed.] Fish distribution. MESA N.Y. Bight Atlas Monogr. 15.

MACDONALD, J. S., AND R. H. GREEN. 1986. Food resource utilization by five species of benthic feeding fish in Passamaquoddy Bay, New Brunswick. Can. J. Fish. Aquat. Sci. 43: 1534–1546.

MCCAIN, J. C. 1968. The Caprellidae (Crustacea: Amphipoda) of the western North Atlantic. U.S. Natl. Mus. Bull. 278.

MURDOCH, W. W., S. AVERY, AND M. E. B. SMYTH. 1975. Switching in predatory fish. Ecology 56: 1094–1105.

PITT, T. K. 1970. Distribution, abundance, and spawning of yellowtail flounder, *Limanda ferruginea*, in the Newfoundland area of the northwest Atlantic. J. Fish. Res. Board Can. 27: 2261–2271.

1976. Food of yellowtail flounder on the Grand Bank and a comparison with American plaice. Int. Comm. Northwest Atl. Fish. Res. Bull. 12: 23–27.

SARS, G. O. 1895. An account of the Crustacea of Norway, Vol. 1: Amphipoda. Christiana and Copenhagen. 711 p.

SCHMITT, R. J., AND S. J. HOLBROOK. 1984a. Ontogeny of prey selection by black surfperch *Embiotoca jacksoni* (Pisces: Embiotocidae): the roles of fish morphology, foraging behavior, and patch selection. Mar. Ecol. Prog. Ser. 18: 225–239.

1984b. Gape-limitation, foraging tactics and prey size selectivity of two microcarnivorous species of fish. Oecologia 63: 6–12.

SEDBERRY, G. R. II. 1980. Food habits prey selectivity, and food resource partitioning of a community of fishes on the outer continental shelf. Ph.D. thesis, The College of William and Mary, Williamsburg, VA. 179 p.

SMITH, F. 1950. The benthos of Block Island Sound. 1. The invertebrates, their quantities and their relation to the fishes., Ph.D. thesis, Yale University, New Haven, CT. 213 p.

URSIN, E. 1973. On the prey size preferences of cod and dab. Medd. Dan. Fisk. Havunders. N.S. 7: 85–98.

URSIN, E., AND W. E. ARNTZ. 1985a. On prey size preference and size-indiscriminate feeding of whiting (*Merlangius merlangus*). Int. Counc. Explor. Sea C.M. 1985/J:6: 16 p.

1985b. The stomach contents of dab (*Limanda limanda*) in the Baltic as indicators of different feeding strategies. Int. Counc. Explor. Sea C.M. 1985/J:7: 9 p.

1985c. On the prey size of cod (*Gadus morhua*) in the Western Baltic. Int. Counc. Explor. Sea C.M. 1985/J:14: 10 p.

ZARET, T. M. 1980. Predation and freshwater communities. Yale University Press, New Haven, CT.

L'incidence d'*Aerococcus viridans* var. *homari* dans le stock naturel de homards *(Homarus americanus)* des îles de la Madeleine (Québec), suite à une épidémie de gaffkémie dans un élevage *in situ*

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En 1982, une importante épizootie de gaffkémie s'est propagée dans un élevage privé de homards (*Homarus americanus*) installé dans la lagune du Havre aux Maisons aux Îles de la Madeleine (Québec, Canada). Cette épidémie s'est soldée par la mort d'environ 40 000 individus. Nos craintes que l'épidémie atteigne le stock naturel se sont révélées non fondées malgré le fait que les conditions semblaient très favorables à la propagation de la maladie. Ainsi, en juin 1983, seulement 2 % des homards échantillonnés autour des Îles (6/300) étaient contaminés. Par la suite (juin 1984), aucun des homards échantillonnés dans la lagune et autour des Îles n'était infecté. L'examen des statistiques de pêche au homard depuis 1979 confirme que le stock n'a pas été atteint par la gaffkémie.

In 1982, gaffkemia appeared in a private lobster (*Homarus americanus*) culture facility located in House Harbour lagoon in Magdalen Islands (Quebec, Canada). It caused the death of about 40 000 lobsters. The outbreak did not expand to the natural stock despite the fact that conditions seemed favourable for the spread of gaffkemia. In June 1983, only 2% of the lobsters sampled around the islands (6/300) were contaminated. By June 1984, no infected individuals were found either in the natural stock or from the private facility. Lobster fishing data from 1979 to 1985 confirm that gaffkemia did not affect natural stock.

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Aerococcus viridans var. *homari* est l'agent étiologique de la gaffkémie, une maladie qui provoque la mort chez le homard (*Homarus americanus*) (Snieszko et Taylor 1947). Ce pathogène est très virulent car il suffit possiblement d'une seule bactérie pour provoquer l'infection d'un individu (Stewart et Cornick 1970). D'ailleurs, plusieurs épidémies ont déjà été enregistrées, causant de lourdes pertes dans des viviers ou des élevages (Edwards *et al.* 1981; Goggins et Hurst 1960; Roskam 1957; Stewart *et al.* 1975).

Jusqu'à présent, cette maladie a surtout été étudiée en laboratoire. On a ainsi caractérisé l'agent pathogène, le développement de la maladie et ses effets sur la physiologie et les composantes biochimiques du homard, et aussi les effets de la température et de la salinité (Aaronson 1956; Cornick et Stewart 1966; Deibel et Niven 1960; Rabin et Hughes 1968; Stewart et Arie 1973; Stewart et Cornick 1970; Stewart *et al.* 1969a; Stewart et Rabin 1970).

En milieu naturel, nos connaissances sur la gaffkémie sont beaucoup plus limitées et souvent difficiles à interpréter. Les hôtes possibles du pathogène ont cependant été identifiés (Stewart 1978). La bactérie a aussi été isolée dans des sédiments vaseux et dans le limon recouvrant les parois des viviers de homards (Goggins et Hurst 1960; Kellog *et al.* 1974; Stewart 1980). De plus on a constaté que le taux d'incidence de la maladie dans les populations de homards variait dans le temps et d'une région à l'autre (Edwards *et al.* 1981; Stewart 1978; Stewart *et al.* 1966; Stewart *et al.* 1975).

L'effet que la gaffkémie pourrait produire sur des stocks de homards est très redouté étant donné la virulence de la ma-

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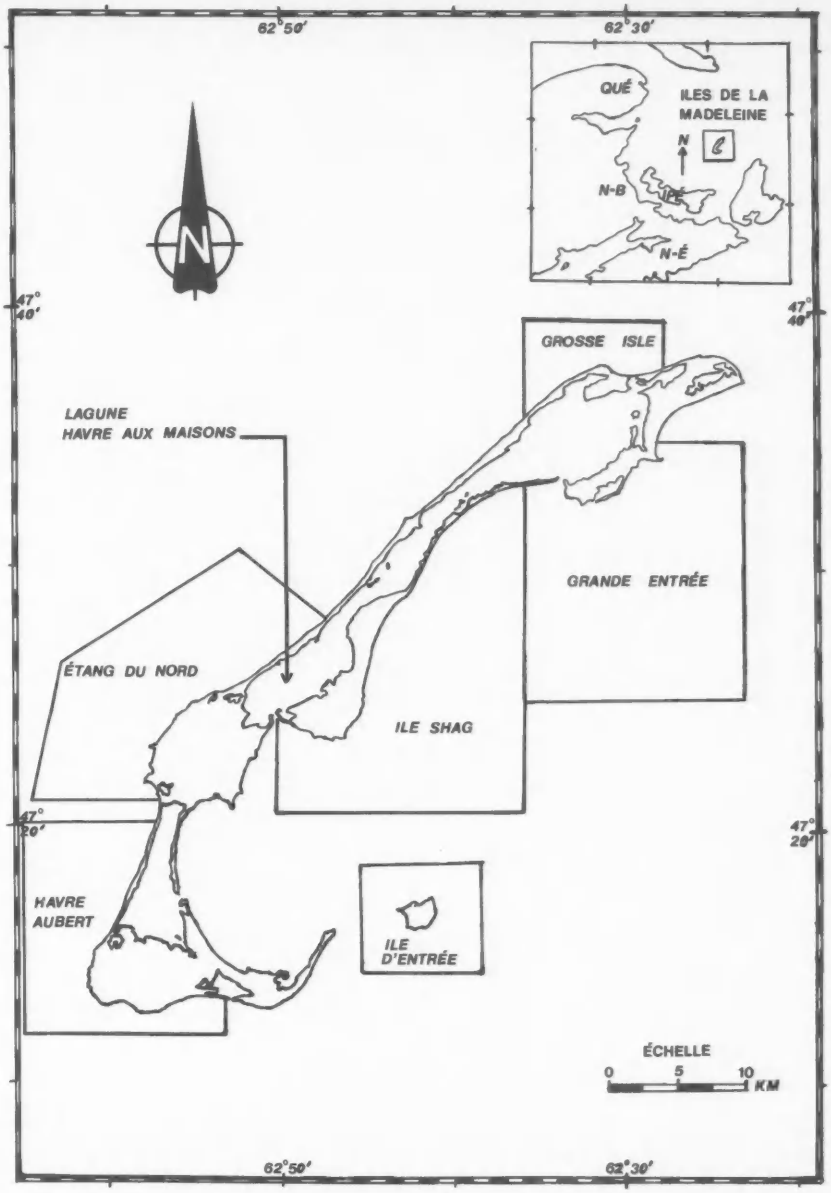

FIG. 1. Carte des îles de la Madeleine indiquant les six grandes zones de pêche et la lagune du Havre aux Maisons.

ladie. Stewart (1978) prétend qu'*Aerococcus viridans* var. *homari* pourrait avoir un effet négatif sur certains stocks naturels en provoquant des mortalités importantes. Kellog *et al.* (1974), après avoir isolé la bactérie dans un estuaire en Californie, considèrent que la menace engendrée par sa présence est évidente et peut mettre en danger la mariculture de certaines espèces. Enfin, Bell et Hoskins (1985) recommandent la vérification et la quarantaine des homards devant être introduits en Colombie-Britanique, afin de protéger la ressource marine compte tenu de l'absence d'*Aerococcus viridans* var. *homari* dans cette région.

Dans le but de documenter les effets réels de la gaffkémie dans une population naturelle, nous rapportons ici la situation qui prévalait aux îles de la Madeleine de 1982 à 1984.

La population de homards des îles de la Madeleine est importante et supporte une pêche côtière dont les débarquements annuels sont de l'ordre de 1 000 t. En 1982, une importante épidémie de gaffkémie s'est propagée dans un élevage de homards placé *in situ*, provoquant la perte d'environ 40 000 homards (Gagnon *et al.* 1984). Nous avons alors examiné le

taux d'incidence d'*Aerococcus viridans* var. *homari* dans le stock naturel et dans l'élevage au cours des deux années subséquentes afin de suivre l'évolution de la maladie.

Méthode

L'archipel des îles de la Madeleine, situé dans le golfe du Saint-Laurent, est caractérisé, entre autres, par la présence de lagunes (fig. 1). C'est dans l'une d'elles, la lagune du Havre aux Maisons, qu'étaient immergées les structures d'élevage de homards appartenant à une compagnie privée. Cette lagune est en contact direct et permanent avec la mer, puisque chaque cycle de marée est caractérisé par un échange de l'ordre de 22 % du volume total de la lagune. Sa superficie a été estimée à 25 km^2 et sa profondeur moyenne est de 1,2 m (Munro et Therriault 1983).

Pour les fins de l'étude, l'ensemble du territoire a été divisé en 6 grandes zones de pêche : Étang du Nord, Grosse Île, Grande Entrée , île Shag, île d'Entrée et Havre Aubert (fig. 1). Ces zones avaient déjà été définies par Dubé et Grondin (1985). L'échantillonnage des captures s'est déroulé en trois étapes : été 1983, automne 1983 et été 1984.

En juin 1983, les homards (*Homarus americanus*) ont été échantillonnés aux ports de débarquement. Ils y avaient été débarqués la journée même, sauf dans le cas d'Étang du Nord où il peut y avoir eu un délai de près de 24 h. Les casiers de pêche étaient levés tous les jours, et dans tous les cas les homards ont été conservés dans des caisses de bois à partir du moment de leur capture. Cinquante homards ont été échantillonnés dans chacune des zones. En juillet et août 1983, il y a eu aussi un échantillonnage sur les homards de la lagune du Havre aux Maisons. Puisque la pêche aux homards y est interdite, les individus échantillonnés provenaient des saisies de casiers de homards faites par les agents des pêcheries du ministère de l'Agriculture, des Pêcheries et de l'Alimentation aux dépens de braconniers. Les prises d'hémolymphe ont été faites dès le retour à terre des agents, soit quelques heures seulement après la sortie de l'eau des casiers. Entre temps, les homards avaient été placés dans des bacs de plastique. Dans ces cas, la durée d'immersion des casiers est évidemment inconnue. Cinquante-sept homards lagunaires ont ainsi pu être analysés.

En octobre 1983, nous avons pu obtenir de 18 à 26 homards par zone sauf pour Grande Entrée. Ces individus nous ont été fournis par M. Pierre Dubé, biologiste au ministère de l'Agriculture, des Pêcheries et de l'Alimentation, qui effectuait des travaux de marquage de homards. Les captures étaient faites à l'aide de casiers de pêche standard. L'échantillonnage était effectué dès le retour à terre de l'équipe de marquage, soit quelques heures après la levée des casiers. Entre temps, les homards étaient gardés dans des bacs de plastique. La durée d'immersion des casiers n'a pas dépassé 48 h.

En juin 1984, nous avons répété l'échantillonnage de l'été 1983 dans les zones de pêche. En plus, nous avons tenu compte du moyen de conservation du homard sur les bateaux de pêche : caisses de bois et viviers de plastique avec circulation d'eau continue. Cinquante homards gardés en viviers ont été échantillonnés en provenance de chacune des zones suivantes : Étang du Nord, Grosse île, Grande Entrée et Havre Aubert. Cinquante individus de chacune des zones de Grande Entrée, de l'île d'Entrée avaient été gardés dans des caisses de bois avant l'échantillonnage.

Nous avons aussi effectué des analyses de contrôle sur des homards de l'élevage commercial situé dans la lagune du Havre aux Maisons. En 1983, 144 homards ont été échantillonnés tandis qu'en 1984, il y en a eu 278. De plus, des analyses ont été effectuées sur les individus morts dans l'élevage (quand le prélèvement d'hémolymphe était encore disponible) afin de déterminer si *Aerococcus viridans* var. *homari* avait été la cause des décès. Il a pu y avoir 23 analyses en 1983, mais seulement 10 en 1984.

Au total, 1 270 homards ont été échantillonnés. Les techniques de prélèvement et d'analyse d'hémolymphe sont celles décrites par Stewart *et al.* (1966).

Résultats

En juin 1983, le taux d'incidence d'*Aerococcus viridans* var. *homari* dans les captures échantillonnées varie de 0 % à 8 % selon les zones (tableau 1). Ceci représente 6 cas confirmés sur 300 individus. Cinq des six cas provenaient de la côte sud des îles de la Madeleine. Un test du chi-carré indique que le taux d'incidence dans la zone de l'île Shag est significativement plus élevé ($p \leq 0{,}05$) que celui observé dans la zone adjacente de Grande Entrée.

Aucun des 57 homards échantillonnés dans la lagune du Havre aux Maisons au cours de l'été 1983 n'a révélé la présence du pathogène (tableau 1).

En octobre 1983, la zone de Grande Entrée n'a pu être couverte. Toutefois, nous n'avons trouvé aucune trace de la présence de la bactérie pathogène chez les 108 homards provenant des cinq autres zones (tableau 1). En juin 1984, toutes les zones ont été échantillonnées mais aucune trace du pathogène n'a été retrouvée parmi les 350 homards examinés (tableau 1).

Les analyses faites en 1983 sur les homards échantillonnés lors des contrôles de routine ont révélé que 1,4 % (2/144) des individus étaient contaminés (tableau 2). Par contre, 30,4 % des homards qui ont pu être autopsiés (7/23) étaient contaminés.

Aucune des 288 analyses en 1984 n'a permis de déceler la présence de l'agent pathogène (tableau 2).

Discussion

De toute évidence, l'épizootie de gaffkémie qui s'est déclarée en 1982 à l'intérieur de l'élevage de homards n'a pas provoqué de mortalité significative dans le stock naturel. D'ailleurs, la maladie était aussi présente dans l'élevage en 1983 mais elle n'a pas dégénéré en épizootie comme l'année précédente. Pourtant en théorie les conditions favorisaient la propagation de la maladie.

L'épizootie de gaffkémie avait causé la perte d'environ 40 000 homards entre le début de juillet et le début de novembre, plus particulièrement en août et en septembre. Le retrait des homards morts dans l'élevage n'avait eu lieu qu'au moment des séances de nourrissage qui étaient espacées de plusieurs jours, voire même plusieurs semaines (Gagnon *et al.* 1984). Les homards morts étaient donc souvent retirés de l'élevage dans un état de décomposition avancé. Or Stewart *et al.* (1969b) mentionnent qu'une quantité considérable d'*Aerococcus viridans* var. *homari* est relâchée dans l'environnement lors de la rupture des tissus d'un homard mort de cette infection, ce qui fournit un véritable inoculum pour la propagation de la maladie. Stewart (1980) indique aussi que la bactérie peut survivre sous forme libre dans les sédiments vaseux. Les fonds vaseux de la lagune sur lesquels étaient déposées les structures

TABLEAU 1. Taux d'incidence de la gaffkémie dans les captures provenant des grandes zones de pêche et de la lagune du Havre aux Maisons (îles de la Madeleine, Québec).

	juin 1983		juillet 1983		octobre 1983		juin 1984	
Zone de pêche	*n*	Incidence (%)	*n*	Incidence (%)	*n*	Incidence (%)	*n*	Incidence (%)
Étang du Nord	50	2	—[a]	—	20	0	50	0[b]
Grosse Île	50	0	—	—	24	0	50	0[b]
Grande Entrée	50	2	—	—	—	—	100	0[b,c]
Île Shag	50	8	—	—	18	0	50	0[c]
Île d'Entrée	50	0	—	—	26	0	50	0[c]
Havre Aubert	50	0	—	—	20	0	50	0[b]
Lagune du Havre aux Maisons	—	—	57	0	—	—	—	—
Total	300		57		108		350	

[a]Zone non échantillonnée.
[b]Homards gardés en vivier sur les bateaux.
[c]Homards gardés dans des caisses de bois sur les bateaux.

TABLEAU 2. Taux d'incidence de la gaffkémie parmi les homards mis en élevage dans la lagune du Havre aux Maisons au cours des saisons d'exploitation (juillet à novembre), 1983 et 1984; échantillonnages de contrôle des individus vivants et vérifications auprès d'individus décédés (autopsies).

	1983		1984	
Prélèvement	*n*	Incidence (%)	*n*	Incidence (%)
Autopsies	23	30,4	10	0
Échantillonnages	144	1,4	278	0
Total	167		288	

d'élevage ont donc pu être contaminés.

La population lagunaire de homards (céphalothorax ⩾ 70 mm) a été évaluée à environ 37 000 individus par Munro et Therriault (1983), et les structures d'élevage étaient placées près de la zone la plus densément peuplée de la lagune (Gagnon *et al.* 1984; Munro et Therriault 1981). Outre la population à proximité des structures d'élevage, de nombreux autres homards lagunaires ont pu être attirés près des structures par la nourriture dispensée aux 64 000 individus en captivité et par la présence de femelles (environ 50 % du lot). Plusieurs homards lagunaires ont donc vraisemblablement été en contact avec l'agent pathogène. Plus encore, Gagnon *et al.* (1984) rapportent qu'environ 7 700 homards se sont échappés de l'élevage au cours de l'été, ce qui représente l'équivalent de 20,8 % de la population lagunaire totale (7 700/37 000). Les contacts avec les homards lagunaires ont dû être nombreux. Or il est fort probable qu'une partie de ces individus étaient contaminés, car l'épizootie a décimé 64 % des homards en captivité. Enfin, les nombreux crabes communs (*Cancer irroratus*) de la lagune, hôtes potentiels du pathogène (Cornick et Stewart 1966), ont pu aussi servir de vecteurs.

Le réchauffement estival de l'eau favorise une grande dispersion de la maladie, car le taux de croissance de la bactérie et l'activité des homards augmentent avec la température (Stewart 1978). Le comportement agressif des homards est d'ailleurs souvent responsable des blessures non cicatrisées nécessaires pour permettre l'infection (Stewart 1980). La lagune du Havre aux Maisons offre donc un milieu favorable à la propagation de la gaffkémie, puisque la température y atteint 20°C au coeur de l'été (Gagnon *et al.* 1984; Poirier et Myrand 1982; ministère de l'Agriculture, des Pêcheries et de l'Alimentation, données inédites).

La lagune est en contact direct avec la mer, et la presque totalité de la population lagunaire de homards entreprend des migrations annuelles caractérisées par une sortie de la lagune en octobre et le trajet inverse en mai. À leur sortie, les homards se dispersent dans toutes les directions sur la côte sud des îles de la Madeleine, mais la majorité demeure à proximité de l'embouchure de la lagune (Dubé 1984). Les homards lagunaires entrent donc en contact avec les homards côtiers, et ce d'autant plus que le printemps, après la migration automnale, seulement 55 % des homards retournent dans la lagune (Munro et Therriault 1983). Il reste alors environ 16 650 homards lagunaires dans la zone côtière (45 % de 37 000). La température de l'eau dans cette zone côtière est aussi favorable à la dispersion de la maladie puisqu'elle atteint 10–15°C au niveau du fond au cours de l'été (Dobson 1981).

Malgré ces conditions propices, seulement 2 % des homards échantillonnés autour des îles de la Madeleine en juin 83 étaient infectés. Le fait que la majorité des individus contaminés proviennent de la zone de l'île Shag pourrait s'expliquer par les mouvements migratoires restreints des homards lagunaires. Nos craintes que le stock naturel ait pu être affecté par l'épidémie de 1982 n'étaient donc pas fondées. L'examen des statistiques de pêche aux îles de la Madeleine depuis 1979 confirme que le stock n'a pas été atteint car les captures annuelles se sont maintenues entre 1 026 042 et 1 423 383 kg (P. Dubé et S. Leblanc, comm. pers.). La proportion des captures provenant de la côte sud sur l'ensemble des prises faites autour de l'archipel est demeurée la même au cours de cette période, soit environ 70 %.

Quelques cas de gaffkémie ont été identifiés en 1983 dans l'élevage. Ces rares cas peuvent vraisemblablement provenir de homards mis en captivité l'année précédente. En effet, un certain nombre de homards placés en captivité en 1982 ont été laissés dans l'élevage au cours de l'hiver 1982–1983 (P. Fradette, C.P. 182, Cap-aux-Meules(Québec) G0B 1B0 comm. pers.). Selon le modèle de Gagnon *et al.* (1984), si des homards ont été contaminés après le mois de septembre, ils sont demeurés vivants jusqu'au printemps avant que la maladie ne reprenne sa progression. Les ajustements techniques opérés par la compagnie (Anonyme 1984) ont ensuite permis d'empêcher la transmission de la maladie à d'autres homards.

Aussi ces quelques cas n'ont pas dégénéré en épizootie, et les pertes ont été négligeables comparativement à l'année précédente. En 1984, aucun cas de gaffkémie n'a été décelé chez les homards en captivité.

L'épidémie apparue dans l'élevage n'a donc pas été suivie par un taux élevé d'incidence d'*Aerococcus viridans* var. *homari* dans le stock naturel de homards, malgré les conditions théoriquement favorables à la dispersion de la maladie. Les résultats obtenus peuvent être interprétés selon les deux schémas suivants :

1) L'épizootie n'a eu aucune conséquence sur le stock naturel, et les taux observés sont plutôt dus à des fluctuations temporelles naturelles semblables à celles observées par Stewart (1980).

2) Les cas de gaffkémie observés résultent d'une propagation réelle mais très limitée de l'épidémie au cours de l'été 83, suivie de sa disparition totale (octobre 1983 et été 1984).

Dans les deux cas, ceci nous amène à conclure qu'en conditions naturelles « normales » (pas de densité excessive), la maladie ne se propagerait pas aussi facilement qu'on aurait pu le craindre. D'ailleurs, l'évolution de la maladie dans l'élevage indique clairement que la gaffkémie ne se propage que lorsque les conditions ambiantes sont très détériorées. En effet, la gaffkémie n'a plus causé de problèmes à partir du moment où des ajustements techniques ont permis de réduire les contacts entre les homards et le nombre de blessures qui pouvaient leur être infligées au cours des manipulations routinières (Anonyme 1984).

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Références

AARONSON, S. 1956. A biochemical-taxonomic study of a marine micrococcus, *Gaffkya homari*, and a terrestrial counterpart. J. Gen. Microbiol. 14 : 478–484.

ANONYME. 1984. Recherche sur les conditions optimales de croissance des homards pour un système d'élevage semi-intensif. Rapport manuscrit inédit présenté au ministère de l'Agriculture, de Pêcheries et de l'Alimentation par Les Crustacés vivants madelinots inc.

BELL, G. R. ET G. E. HOSKINS. 1985. Absence of the lobster pathogen *Aerococcus viridans* in Dungeness crabs (Cancer magister) taken from Vancouver Harbor, British Colombia, Aquaculture 47: 263–265.

CORNICK, J. W. ET J. E. STEWART. 1966. Microorganisms isolated from the hemolymph of the lobster (*Homarus americanus*). J. Fish. Res. Board Can. 23 : 1451–1454.

DEIBEL, R. H. ET C. F. NIVEN JR. 1960. Comparative study of *Gaffkya homari*, *Aerococcus viridans*, tetrad-forming cocci from meat-curing brines, and the genus *Pediococcus*. J. Bacteriol. 79 : 175–180.

DOBSON, D. 1981. Longterm temperature monitoring program 1980. Institut océanographique de Bedford (Nouvelle-Écosse). Data Ser. B1-D-81-3.

DUBÉ, P. 1984. Analyse des déplacements du homard (*Homarus americanus*) sur les côtes des îles de la Madeleine, à partir des données de marquage et de recaptures, de 1978 à 1983, CSCPCA Doc. rech. 84/37.

DUBÉ, P. ET P. GRONDIN. 1985. Maturité sexuelle du homard (*Homarus americanus*) femelle aux îles de la Madeleine. CSCPCA Doc. rech. 85/85.

EDWARDS, E., P. A. AYRES ET M. L. CULLUM. 1981. The incidence of the disease gaffkemia in native (*Homarus gammarus*) and imported lobsters (*Homarus americanus*) in England and Wales. Int. Counc. Explor. Sea, Shellfish Comm. 1981/K12.

GAGNON, M., P. FRADETTE ET P. BÉLAND. 1984. Suivi d'une expérience d'élevage de homards (*Homarus americanus*) de taille commerciale en milieu lagunaire aux îles de la Madeleine, en 1982. Can. Tech. Rep. Fish. Aquat. Sci. f1286.

GOGGINS, P. L. ET J. W. HURST JR. 1960. Progress report on lobster Gaffkyaremia (red tail), Maine Dep. Sea Shore Fish., p. 1–9 (inédit).

KELLOG, S., J. F. STEENBERGEN ET H. C. SCHAPIRO. 1974. Isolation of *Pediococcus homari*, etiological agent of gaffkemia in lobsters, from a California estuary. Aquaculture 3 : 409–413.

MUNRO, J. ET J. C. THERRIAULT. 1981. Abondance, distribution, mobilité et fréquence de mue de la population de homards des lagunes des îles de la Madeleine. Can. Tech. Rep. Fish. Aquat. Sci. 1034.

1983. Migrations saisonnières du homard (*Homarus americanus*) entre la côte et les lagunes des îles de la Madeleine. Can. J. Fish. Aquat. Sci. 40 : 905–918.

POIRIER, L. ET B. MYRAND. 1982. Élevage de la moule bleue, *Mytilus edulis*, dans les lagunes des Îles de la Madeleine (Québec). Trav. Pêch. Qué. 49.

RABIN, H. ET J. T. HUGHES. 1968. Studies on host–parasite relationships in gaffkemia. J. Invertebr. Pathol. 10 : 335–344.

ROSKAM, R. T. 1957. Gaffkemia, a contagious disease in *Homarus vulgaris*. Int. Counc. Explor. Sea, Shellfish Comm. Rep. Fl.

SNIESZKO, S. F. ET C. C. TAYLOR. 1947. A bacterial disease of the lobster (*Homarus americanus*). Science (Wash. DC) 105 : 500.

STEWART, J. E. 1978. The lobster disease, gaffkemia, in relation to fisheries management. Int. Counc. Explor. Sea, Shellfish Comm. Rep. F16.

STEWART, J. E. 1980. Diseases, p. 301–342. Dans J. S. Cobb et B. F. Phillips [ed.]. The biology and management of lobsters, I. Physiology and behavior. Academic Press, New York, NY.

STEWART, J. E. ET B. ARIE. 1973. Depletion of glycogen and adenosine triphosphate as major factors in the death of lobsters (*Homarus americanus*) infected with *Gaffkya homari*. Can. J. Microbiol. 19 : 1102–1110.

STEWART, J. E. ET J. W. CORNICK. 1970. Disease among stored lobsters (Gaffkemia). Fish. Res. Board Can. News Ser. Circ. 41.

STEWART, J. E., J. W. CORNICK, D. I. SPEARS ET D. W. MCLEESE. 1966. Incidence of *Gaffkya homari* in natural lobster (*Homarus americanus*) populations of the Atlantic region of Canada. J. Fish. Res. Board Can. 23 : 1325–1330.

STEWART, J. E., J. W. CORNICK ET B. M. ZWICKER. 1969a. Influence of temperature in Gaffkemia, a bacterial disease of the lobster (*Homarus americanus*). J. Fish. Res. Board Can. 26 : 2503–2510.

STEWART, J. E., A. DOCKRILL ET J. W. CORNICK. 1969b. Effectiveness of the integument and gastric fluid as barriers against transmission of *Gaffkya homari* to the lobster *Homarus americanus*. J. Fish. Res. Board. Can. 2611–2614.

STEWART, J. E. ET H. RABIN. 1970. Gaffkemia, a bacterial disease of lobsters (genus *Homarus*), p. 431–439.. Dans S. F. Sniezko [ed.] A symposium of diseases of fishes and shellfishes. Spec. Publ. f5. American Fisheries Society, Washington, D.C.

STEWART, J. E., B. M. ZWICKER ET B. ARIE. 1975. Status report on Gaffkemia in lobsters in Atlantic Canada. Int. Counc. Explor. Sea. C.M. 1975/K:20.

Behavioral and Biochemical Studies of Onset and Recovery from Acid Stress in Arctic Char (*Salvelinus alpinus*)

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Jones, K. A., S. B. Brown, and T. J. Hara. 1987. Behavioral and biochemical studies of onset and recovery from acid stress in Arctic char (*Salvelinus alpinus*). Can. J. Fish. Aquat. Sci. 44: 373–381.

The time course of acid stress was followed in Arctic char (*Salvelinus alpinus*) exposed to pH 4.5 (HCl) for 2 wk and then returned to control conditions (pH 7.8). Behavioral parameters (activity, thigmotaxis, appetite, and attraction to a food extract) and blood parameters (hematocrit and plasma Cl^-, Na^+, osmolality, protein, cortisol, and glucose) were monitored. Reaction to the acid was evident in all parameters. Fish were initially hyperactive but became hypoactive with continued exposure. Thigmotaxis was generally greater in the acid-stressed fish than the controls. Feeding intensity and attraction to food extract were depressed throughout the exposure, but periods of partial recovery occurred. Hematocrit, protein, cortisol, and glucose increased, while osmolality, Cl^-, and Na^+ decreased in acid-exposed fish. Partial recovery occurred in some blood parameters during the latter part of the exposure. After return to control conditions, behavioral and blood parameters except cortisol recovered within 2 wk but might have recovered earlier if fish had not contracted a *Saprolegnia* infection. Extract attraction was negatively correlated with hematocrit, protein, cortisol, and glucose and positively correlated with plasma Cl^-. Activity was negatively correlated with plasma protein and glucose. Thigmotaxis was not correlated with any blood parameter.

Les auteurs ont suivi le développement de la réaction à l'acide en fonction du temps chez des ombles chevaliers (*Salvelinus alpinus*) exposés à un pH 4,5 (HCl) pendant 2 sem puis retournés à des conditions témoins (pH 7,8). Ils ont surveillé les paramètres du comportement (activité, thigmotaxie, appétit et attirance vers un extrait d'aliment) et les paramètres sanguins (hématocrite, concentrations de Cl^- et Na^+ plasmatiques, osmolalité, protéine, cortisol et glucose). Tous les paramètres ont révélé une réaction à l'acide. Au début, les poissons étaient hyperactifs mais sont devenus hypoactifs après une exposition continue. La thigmotaxie était généralement plus élevée chez les poissons soumis à une charge d'acide que les poissons témoins. L'intensité de l'alimentation et l'attirance vers des extraits de nourriture ont diminué pendant toute l'exposition quoique des périodes de récupération partielle aient été observées. Les teneurs en hématocrite, en protéine, en cortisol et en glucose ont augmenté tandis que l'osmolalité et les concentrations de Cl^- et de Na^+ ont baissé chez les poissons soumis à une charge d'acide. On a observé une récupération partielle de certains paramètres sanguins au cours de la dernière partie de l'expérience. Le retour aux conditions témoins a entraîné un retour aux taux normaux des paramètres du comportement et du sang, sauf dans le cas du cortisol, en moins de 2 sem; ils seraient peut-être revenus plus tôt à la normale si les poissons n'avaient pas été atteints d'une infection de *Saprolegnia*. L'attirance vers des extraits de nourriture était en corrélation négative avec les teneurs en hématocrite, en protéine, en cortisol et en glucose et en relation positive avec la teneur en Cl^- plasmatique. L'activité était en corrélation négative avec la teneur en protéine et en glucose plasmatiques. La thigmotaxie n'était liée à aucun paramètre sanguin.

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Chronic acid exposure, even at sublethal levels, is sufficient to induce marked disturbances in the histology, physiology, and behavior of salmonids (Daye and Garside 1980; Fromm 1980; Jones et al. 1985a). Although these responses are indicative of stress, at least some may actually constitute adaptive mechanisms for preventing further disturbance. For example, reduced activity, a frequent characteristic of acid stress in fishes (Beamish 1972; Mount 1973; Dively et al. 1977; Falk and Dunson 1977; Swarts et al. 1978; Peterson and Martin-Robichaud 1983; Ellgaard and Gilmore 1985; Jones et al. 1985a), could enhance survival because exercise potentiates acid toxicity (Graham and Wood 1981). Nevertheless, despite possible short-term benefits, some responses (e.g. cessation of feeding and reduced social interactions) cannot be continued indefinitely without eventually leading to death of fish or extinction of the population even at physiologically tolerable pH levels. Therefore, it is not surprising that the year-round low pH of some freshwaters has prevented the invasion of salmonids (Rahel and Magnuson 1983), or that the acidification of normally supportive waters leads to the gradual disappearance of resident salmonids (EIFAC 1969; Almer et al. 1974; Muniz and Leivestad 1980; Somers and Harvey 1984).

In other waters, pH drops to stressful levels for only brief periods, as during acidic snowmelts and heavy acidic rainfalls (Leivestad and Muniz 1976; Jeffries et al. 1979). Although the salmonids will orient away from high concentrations of acid (Höglund 1961; Johnson and Webster 1977; Jones et al. 1985b), refuge from acid pollution is not always available, and

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inevitably some populations are forced to endure the stressful conditions. Survival in these waters will depend on the fish's ability to withstand the brief exposure to high acidity and to recover normal function once the pH returns to tolerable levels. Hence, it becomes important to know the rates at which a fish succumbs and recovers if we are to understand the relative impact of chronic versus episodic occurrences of acid pollution. Some physiological work on the rates of onset and/or recovery from acid stress has already been done on rainbow trout (*Salmo gairdneri*) (Booth et al. 1982: Brown et al. 1984, 1986) and brown trout (*Salmo trutta*) (McWilliams 1980). Equivalent work has not been conducted on the Arctic char (*Salvelinus alpinus*) and these rates have not been determined for behavior in any salmonid.

The purpose of this study was twofold. First, we sought to determine the rates of onset and recovery from acid stress in Arctic char. Second, we sought to establish whether a correlation exists between locomotor behavior and blood chemistry at the level of the individual.

Materials and Methods

Experimental Animals

The history of the fish, holding conditions, and water quality are described in Jones et al. (1985a). Briefly, a group of 180 juvenile Arctic char, 14–17 cm in total length and 40–50 g in weight, were transferred from the Department of Fisheries and Oceans' Rockwood Experimental Fish Hatchery in Gunton, Manitoba, to the Freshwater Institute where the fish were divided into two groups of 130 and 50 individuals. The larger group was placed in a 180-L fiberglass tank, while the smaller group was placed in two 40-L aquaria. Both groups were supplied with dechlorinated filtered Winnipeg city water (12.5°C, pH 7.8) at a minimum rate of 2 $L \cdot g\ fish^{-1} \cdot d^{-1}$ (Sprague 1969). The fish received a maintenance ration (0.5% body weight) of Martin's Trout Feed daily.

The larger group served as the acid-exposed group and the smaller group as the controls. The fish were acclimated to laboratory conditions for 7 d. By this time the fish had begun to feed regularly. The test group was then switched to water previously stripped of it bicarbonates with H_2SO_4 and titrated with NaOH to pH 6.3 (Brown et al. 1984). This prevented an accompanying increase in CO_2 tension when the water was later acidified. Periodic checks of pH showed that the change in water chemistry was essentially complete within 3 h. Test fish were held in this water for the next 5 d. Control fish remained in the decarbonated water throughout the experiment.

Behavioral Tests

Testing began on September 9, 1983 (day 0), and continued for 30 d. On that day, seven control fish were selected at random and their locomotor performance monitored as described earlier (Jones et al. 1985a). Each char was permitted to swim freely within a behavioral trough (200 × 33 × 16 cm) while an analogue of its unit position (0–100) along the horizontal axis was recorded on a strip chart for 8 min. After this time a food extract (filtered solution of trout feed, 0.01 $g \cdot L^{-1}$) was infused into the areas between units 35 and 55 at a rate of 0.5 $mL \cdot min^{-1}$. The water flow within the trough was such that the extract formed a plume of treated water lying across the path of the fish. The subject's movements were then recorded for an additional 8 min after its initial contact with the extract plume. Each char was tested alone and only once. Strip chart recordings were later digitized and the information was used to calculate three locomotor variables: total distance traveled during the first 8-min period; total time accumulated in the areas between units 0 and 10 and 90 and 100 during the first period; and the time spent in the chemical field (units 35–55) during the infusion of the extract. The three variables were taken to represent activity, thigmotactic intensity (the tendency to remain near the ends of the trough), and the strength of attraction for the extract, respectively.

An additional set of nine control fish was tested in the same manner 24 d later to determine if a significant change had occurred in the control group during the course of study. On day 2 (5 d after the switch to decarbonated water) the pH within the exposure tank was lowered within a 2-h period to 4.5 by adding H_2SO_4. The pH was held at this level for the next 2 wk. Beginning on day 3 and continuing through day 11, five acid-treated fish were chosen daily and tested in the manner described for the controls. Additional groups of five fish were tested on days 13 and 15. On day 16 the pH within the exposure tank was raised to 7.0 in the course of 5 h by adding NaOH. The water supply was then switched back to normal laboratory water (pH 7.8). Test fish remained in this water for the remainder of the experiment. Postexposure tests were conducted on groups of five fish 3, 7, and 14 d after their return to laboratory water (days 19, 23, and 30, respectively).

Blood Parameters

At the completion of the second monitoring period, each subject was removed from the trough, stunned with a blow to the head, and its blood collected in a heparinized centrifuge tube after removing the tail just above the caudal peduncle. The entire process required less than 90 s and usually less than 60 s. Part of the sample was used to determine hematocrit. The remainder was centrifuged and its plasma withdrawn, aliquoted into plastic vials, and frozen until analyzed. Plasma protein, glucose, and cortisol were assayed according to the procedures described by Brown et al. (1984). If sufficient plasma remained after these three tests, then the excess was further assayed for Cl^-, Na^+, and/or osmolality using the methods of Brown et al. (1986). For reasons unrelated to the experiment, no measurements were taken on the plasma electrolytes and osmolality of the postexposure samples. Changes in hematocrit and plasma protein, electrolytes, and osmolality can be considered as indicators of osmoregulatory, ionic, and/or blood fluid responses to acidification. Changes in glucose reflect the mobilization of energy reserves and may also act as an osmoregulatory mechanism. Cortisol is a measure of activity within the hypothalamus–pituitary–interrenal axis in response to stress.

Statistics

Daily means and standard deviations were calculated for the three behavioral parameters (activity, thigmotaxis, extract attraction) and the seven blood parameters (Cl^-, Na^+, osmolality, hematocrit, protein, cortisol, and glucose). Means from the two control days (0 and 24) were compared by two-sample *t*-tests (unpaired, two-tailed) and, if no significant difference was found, the two days were pooled to make a stronger statistical control from that parameter. In the case of Cl^-, Na^+, and osmolality, only control day 0 was used.

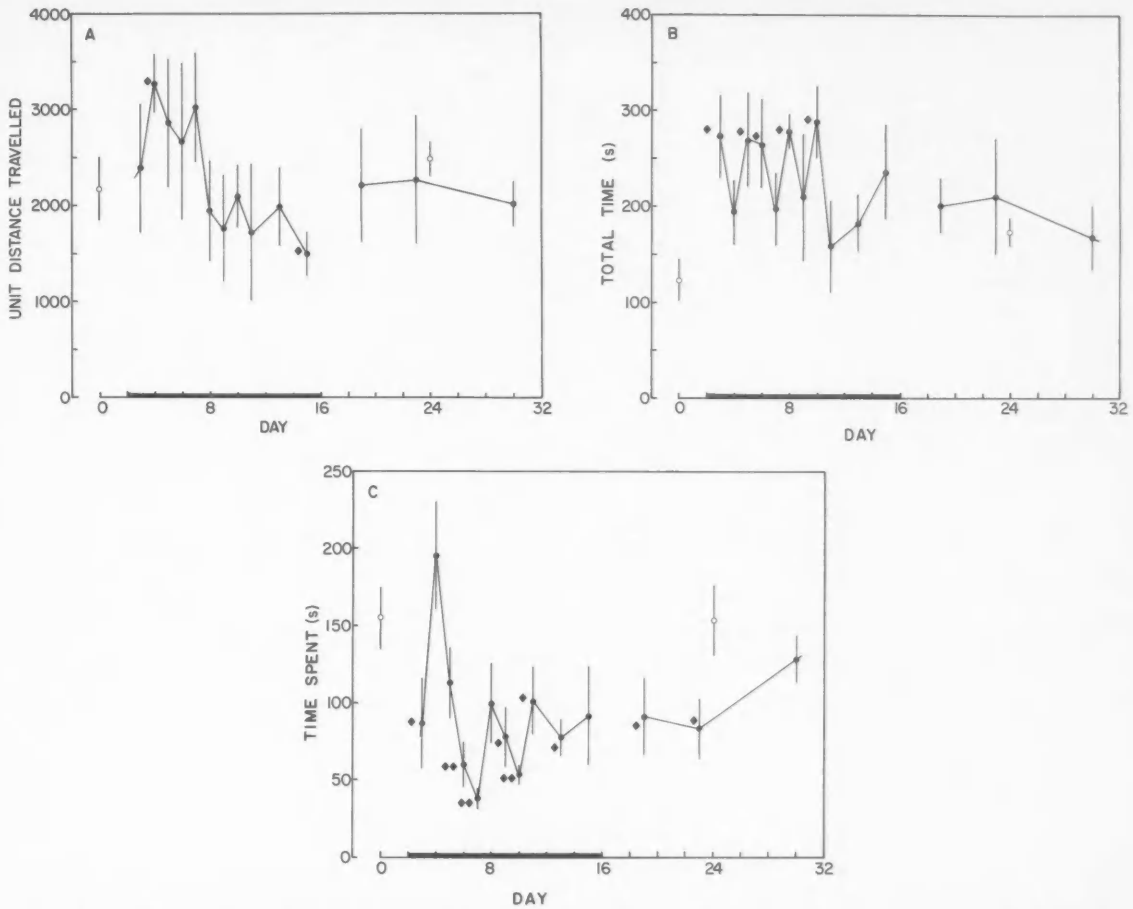

FIG. 1. Onset and recovery from acid stress in three behavioral parameters: (A) activity; (B) thigmotaxis; (C) food extract attraction. The period of acid exposure is shown here and elsewhere by the heavy black line on the horizontal axis. Open symbols are control fish; closed symbols are treated fish. Each point represents the daily mean (± 1 SE). Means significantly different from control values are indicated by solid triangles (◆ = 0.05 level; ◆ ◆ = 0.01 level).

Individual exposure and postexposure days were them compared against the controls or combined controls (two-sample *t*-tests) to determine significant differences. Linear trends within the data were analyzed for significance through simple linear regressions.

Finally, physiological/physiological and physiological/behavioral parametrical pairs were tested for their correlation which was considered significant when the probability of exceeding the test statistic was <0.05.

Results and Discussion

Behavior

Control and preexposure behavior

On day 0 the average control char traveled a distance of 2175 units in the initial 8-min monitoring period (Fig. 1A). It accumulated 123 s in the end sections (Fig. 1B), while 86 s was spent in the treatment area in the absence of the extract (not shown). During infusions of the extract, time spent in the same area rose to 155 s (Fig. 1C). Day 24 controls did not differ significantly from day 0 controls in any behavioral parameter. Control fish in holding fed readily and required roughly 2.0–2.5 min to consume their daily ration (Fig. 2). Prior to acid exposure, test fish in holding (pH 6.3) were indistinguishable from the controls in their general behavior and ration consumption time.

Behavior during acid exposure

The mean activity of the test fish while in the trough was similar to that of the controls on day 3 (Fig. 1A). This was not for a lack of effect of the acid, but because the immediate response varied considerably among the fish. Of the five char tested, two were similar to the controls, two were hyperactive, and one exceptionally hypoactive. However, with continued exposure most fish became hyperactive. On day 4 all of the char sampled were hyperactive, and the difference from the controls was highly significant. Activity then remained elevated for the next few days, although hypoactive individuals could occasionally still be found. It should be noted that

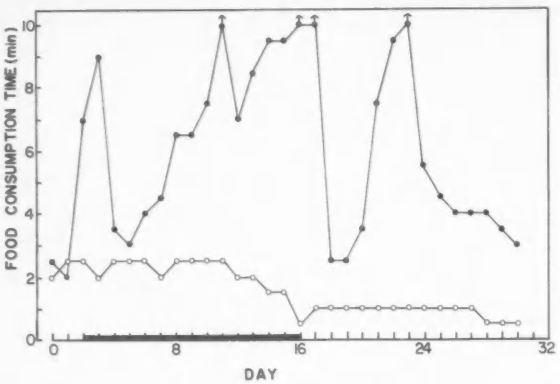

FIG. 2. Effects of acid stress on feeding intensity (appetite) measured as the amount of time required by the group to fully consume a daily ration (0.5% body weight) of trout feed. Symbols are as in Fig. 1.

hyperactivity was only seen in the trough. Unsampled test char in the exposure tank were noticeably quiescent and usually found lying rigidly still en masse on the bottom. Thus, the hyperactivity seen in the trough was likely a reaction by the sampled individuals to handling stress. Hyperactivity was almost always accompanied by a heightened degree of excitability seen as an increased sensitivity to being startled, sudden bursts of swimming, and frequent attempts to leave the trough by "climbing" its walls. After day 4 a number of char became hypoactive. Activity decreased significantly between days 4 and 15 ($r = -0.406$, $F_{1,48} = 9.47$, $p < 0.01$) at an overall rate of 150 units·d^{-1}. Day 15 was significantly lower than controls.

Arctic char exhibited a greater thigmotaxis after 24 h of exposure, accumulating an average of 275 s at the ends of the trough (Fig. 1B). Thereafter, thigmotaxis fluctuated considerably with time, showing no apparent tend towards increasing or decreasing.

After 24 h of exposure, Arctic char significantly reduced their time spent in the chemical field during extract infusions (Fig. 1C). This decrease in time spent had two causes: the stronger thigmotaxis which caused the fish to spend less time in the central sections of the trough in general, and a clear loss of interest in the extract. Concomitantly, food consumption time in the exposure tank rose from 2 min on day 1 to 7 min on day 2, indicating a depressed feeding intensity (Fig. 2). Appetite in the stressed group decreased even further 24 h later. Following their initial depression in extract attraction and feeding intensity, acid-stressed char showed a renewed interest in the extract and daily ration on day 4 (Fig. 1C and 2). The improvement of the fish suggests that they had recovered from their initial shock, possibly as the result of some physiological adjustment to the acid. However, their recovery was short-lived. Attraction steadily declined over the next 3 d while, after day 5, the time required to consume the food ration increased over the next 6 d. Two less substantial recoveries may also have occurred on day 8 (day 7 vs. day 8, $t_8 = 2.36$, $p = 0.05$) and day 11 (day 10 vs. day 11, $t_8 = 2.22$ $p \leq 0.05$). There was no concomitant recovery in appetite on either day, although there may have been on day 12. At the end of the 2-wk exposure the stressed char required at least 10 min (observation was discontinued at that time) to consume their ration. Control fish maintained or even increased their feeding intensity during the experiment.

The behavioral changes described here generally agree with those of an earlier study where Arctic char were exposed for a minimum of 2 wk to pH 4.5 prior to being tested (Jones et al. 1985a). The major exception is that activity in the trough was reported there to be depressed by acid stress. By following the time course of acid stress, we have determined that the effects of acid are actually biphasic: an initial period of hyperactivity, caused by a heightened sensitivity to handling stress, followed by a secondary gradual shift towards hypoactivity. We have also established that there can be at least an initial brief period of recovery and perhaps less substantial secondary recoveries during the course of exposure. The behavior of the char during the first recovery, particularly once they were over their initial shock, resembled that of char chronically exposed to pH 5.0. The latter group is characterized by hyperactivity and a moderately depressed extract attraction (Jones et al. 1985a). The similarities between the two groups lead to the conclusion that the char in the more acidic environment had initially undergone the same compensatory physiological adjustments as those in the milder one. However, the continued exposure to the higher acidity eventually caused these compensations to fail and required the fish to undergo further physiological and behavioral changes to resist the acid.

As noted earlier, changes in activity during acid stress have been frequently reported. Given the wide array of taxonomic groups which show the characteristic, it is evident that the response is typical of fish in general. A similar case can be made for the cessation or depression in feeding (Beamish 1972; Dively et al. 1977; Swarts et al. 1978; MacFarlane and Livingston 1983). To our knowledge, changes in thigmotaxis during stress have not been studied in any other fish species; no conclusions can presently be drawn as to how common that response may be. Regarding the reduction in food extract attraction, a recent study by Lemly and Smith (1985) demonstrated that the fathead minnow (*Pimephales promelas*), a species relatively sensitive to acidification, ceased its locomotor reactions to chemical feeding stimulants at a pH as high as 6.0. Their work confirms that the depressed response to chemical feeding stimulants is not restricted to Arctic char or the salmonids. Actually, a potentially wide range of chemically mediated behaviors in fish could be adversely affected by acid stress, since, in addition to disturbing physiological norms, high levels of acid destroy the olfactory epithelium (Daye and Garside 1980) and modify the olfactory response to chemical stimuli (Hara 1976; R. E. Evans, Freshwater Institute, Winnipeg, Man., pers. comm.). Thus, chemical communication could be disrupted at any of several points, ranging from chemosensory impairment to the masking or counteraction of biologically relevant signals (see Hara et al. 1983).

Behavior during postexposure

Within 24 h (day 17) following their return to laboratory water, char in the exposure tank began displaying a renewed vitality in their behavior (direct observation). Activity appeared to be near-normal after 1 d and normal after 2 d. Feeding intensity did not recover as quickly. After 1 d in nonstressful conditions, the test fish still required more than 10 min to consume their daily ration (Fig. 2). Considerable improvement was indicated on the next day when the ration was consumed in only 2.5 min. Thus, the general behavior of

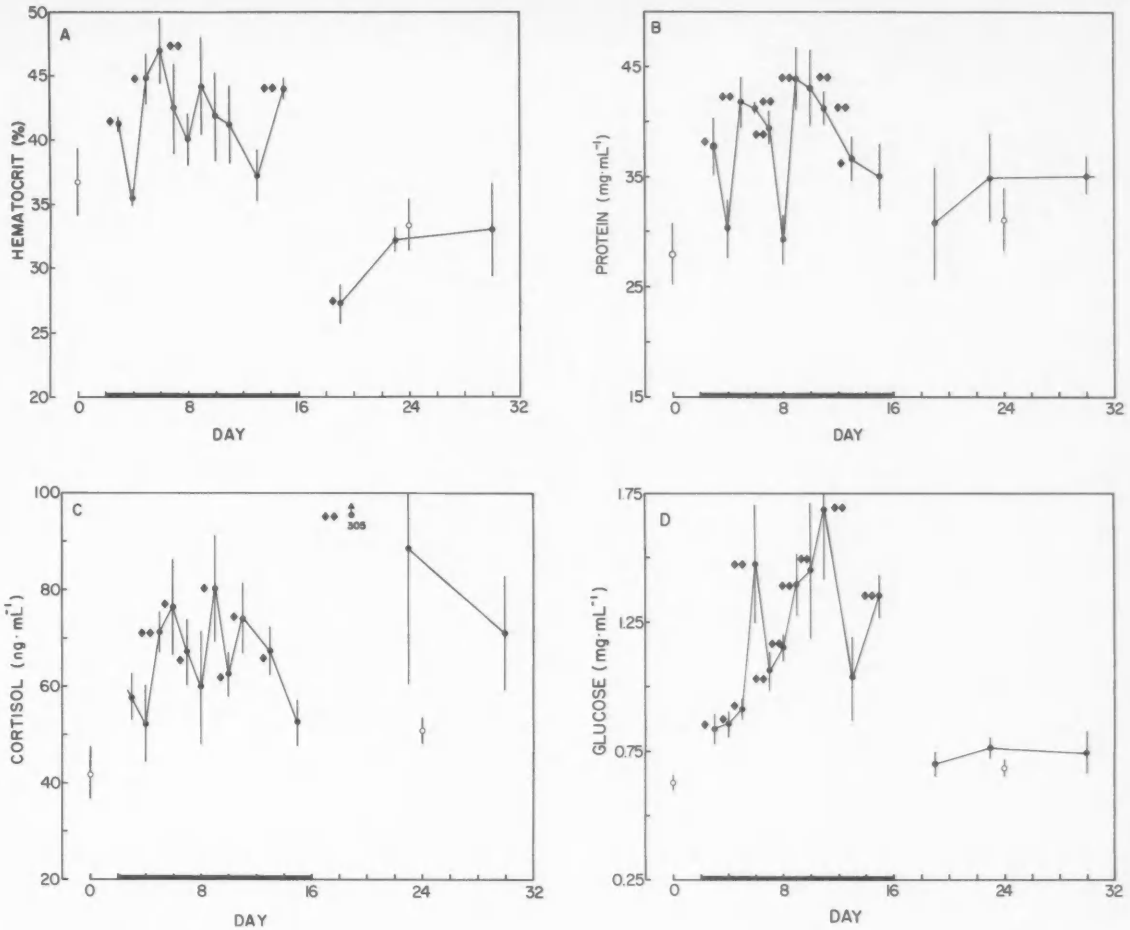

FIG. 3. Onset and recovery from acid stress in four blood parameters; (A) hematocrit; (B) plasma protein; (C) plasma cortisol; (D) plasma glucose. Symbols are as in Fig. 1.

the unsampled char suggested that their condition was rapidly approaching normality after 48 h of nonstressful conditions. However, the health of these fish suffered a setback when they became infected with the fungus *Saprolegnia*. Therefore, time to recovery from the effects of acidification may be overestimated. Symptoms of the infection were evident 4 d following return to control water (day 20) and several fish from this group died soon after. Probably because of the infection, feeding behavior declined once more. After 7 d (day 23), feeding intensity was minimal. The infection was left untreated except that all individuals with visible signs of the fungus were removed and destroyed. The surviving fish eventually recovered their appetite before the conclusion of the experiment (Fig. 2). The control fish did not suffer any disease, and their feeding behavior was unaffected throughout the course of the study. Other investigators have also observed an increased susceptibility of stressed fish to diseases (Mazeaud 1981; Wedemeyer and McLeay 1981).

After 3 d of recovery (day 19), mean activity and thigmotaxis in the trough had returned to preexposure levels (Fig. 1A and 1B). Nevertheless, there was evidence that the fish had not recovered by this early date: the variability in activity continued to be high for at least 7 d after nonacidic conditions were restored, and mean time spent in the end section, although already not statistically different from the controls on day 19, approached more normal values with time. Furthermore, attraction to food extract remained significantly depressed after 1 wk in laboratory water. Although no fish showing signs of the fungus was tested, this discrepancy was possibly caused by the fungal infection. After 2 wk the char exhibited a level of attraction which was statistically indistinguishable from the controls. Thus, on the basis of the tests in the behavioral trough, full recovery from acid stress required 7–14 d following the return to nonstressful conditions.

Blood Parameters

Control char

On day 0, control char had an average hematocrit of 37%

and plasma concentrations of 28 mg protein·mL^{-1} 42 ng cortisol·mL^{-1} and 0.63 mg glucose·mL^{-1} (Fig. 3). The values for hematocrit, protein, and glucose agreed with blood samples of control char (N = 10) taken directly from their holding tank (35%, 33 mg·mL^{-1}, and 0.71 mg·mL^{-1}, respectively), as well as with the normal levels reported for other species (Lee et al. 1983; Brown et al. 1984). Elevated cortisol levels seen here (day 0, 42 ng·mL^{-1}) were no doubt caused by the handling stress associated with the test procedure (Mazeaud et al. 1977; Strange et al. 1977; Davis and Parker 1983) accentuated by acid stress (Barton et al. 1985). Day 24 control char did not differ statistically from the day 0 controls in any of these four parameters. This suggests that no significant physiological changes had occurred during the course of the experiment, although rapid changes in such labile components like cortisol cannot be ruled out. When the four parameters were paired and regressed against each other, none of them were correlated at the level of the individual.

Control char were also characterized by having plasma Na^+ and Cl^- concentrations of 152 and 134 mmol·L^{-1} respectively, and a blood osmolality of 308 mosmol·kg^{-1} (Fig. 4). These values agreed with those reported by McWilliams (1980) for brown trout and by Brown et al. (1986) for rainbow trout. Giles et al. (1984) reported slightly lower values in rainbows. No correlations were attempted with the control values of these parameters due to the small number of observations.

During acid exposure

After 24 h of acidification, hematocrit averaged around 41%, a value significantly higher than the combined controls (Fig. 3A). By 48 h, hematocrit had falled to 35%. Presumably, these were passive changes associated with the loss of blood fluid (Milligan and Wood 1982) and erythrocyte swelling due to stress (Soivio and Nikinmaa 1981). Hematocrit then rose to even higher levels by day 5; a peak value of 47% was recorded on day 6. Thereafter, hematocrit exhibited a rough trend towards progressively lower levels through day 13. On day 15 it was again found to be elevated.

Plasma protein behaved much like hematocrit for the first 3 d of exposure, i.e. an initial significant increase, a subsequent decrease to control levels, finally followed by a second rise to even higher levels (Fig. 3B). Again, these changes likely reflect fluctuations in blood fluid. It should not be ruled out, however, that protein, particularly some enzymes, could have played a more specific role in the reaction and acclimation to the acid. Unlike hematocrit, plasma protein repeated the above pattern of decrease and increase between days 7 and 9. It then steadily decreased for the remainder of the exposure.

Cortisol, the most labile of the blood parameters, was significantly higher than the controls 24 h after acidification (Fig. 3C). It remained elevated throughout the majority of the exposure but fluctuated considerably. Between days 5 and 13, cortisol had an overall average value of 69 ng·mL^{-1}, individual values ranging from 41 to 105 ng·mL^{-1}. Cortisol appeared to have decreased to control levels by day 15.

Plasma glucose was also significantly elevated after 24 h of exposure, the mean exceeding the control level by 32% (Fig. 3D). In general, glucose levels increased with time, rising at 9.7 mg·mL^{-1}·d^{-1} between days 3 and 11 (r = 0.585, $F_{1,43}$ = 22.3, $p \leq 0.01$). Individuals with exceptionally high values were found as early as day 6 when three fish were measured at 1.56, 1.62, and 2.18 mg·mL^{-1}, respectively. By

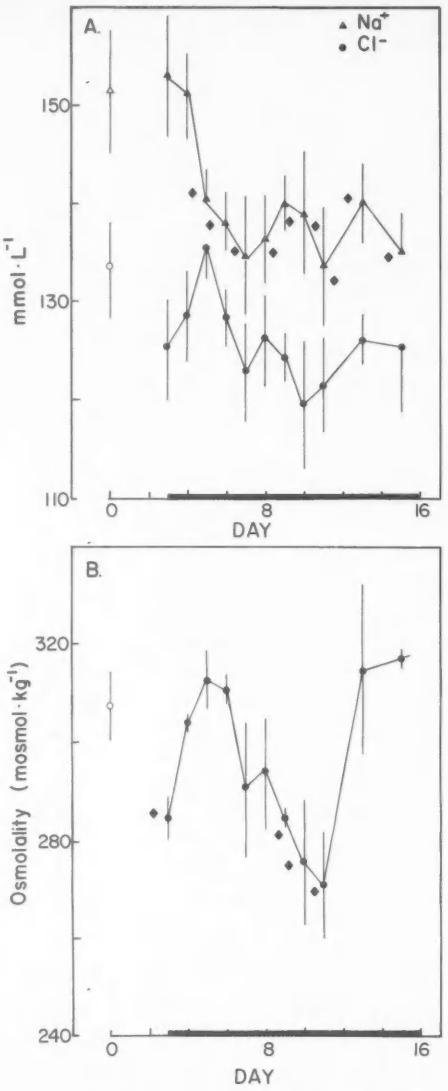

FIG. 4. Onset of acid stress in (A) plasma Cl^- and Na^+ and (B) plasma osmolality. Symbols are as in Fig. 1.

day 9 the majority of individuals lay within this range. Substantially lower values were recorded on day 13, but by day 15 glucose had risen once more.

No statistically significant changes in blood electrolytes were detectable until 72 h (Fig. 4A). By that time, Na^+ had fallen from a mean value of 153 mmol·L^{-1} to 140 mmol·L^{-1}. Mean Na^+ levels then remained around this level for the duration of the exposure, averaging 137 mmol·L^{-1} overall. No single test day's results for Cl^- differed significantly from the controls. However, the combined results of days 6–15 were significantly lower than the controls (t_{38} = 3.41, p = 0.005), confirming that the fish had indeed lost plasma Cl^-. Our results from Fig. 4A indicate that this loss had begun as early as day 6.

Blood osmolality was initially depressed by acidification but had returned to control levels by 48 h (Fig. 4B). After day 6, blood osmolality feel steadily to its lowest mean level of 271 mosmol·kg^{-1} on day 11. The overall rate of decrease was 7.2 mosmol·d^{-1} ($r = -0.576$, $F_{1,23} = 11.4$, $p < 0.01$). The sudden return of this parameter to control levels on days 13 and 15 was not explicable in terms of any accompanying changes in Na^+ and Cl^-.

Numerous pairs of blood parameters that had not been correlated before acidification were correlated after. When tested at the level of the individual the following were significant: Cl^- and Na^+ ($r = 0.702$, $p \leq 0.001$), Cl^- and osmolality ($r = 0.802$, $p \leq 0.001$), Na^+ and osmolality ($r = 0.653$, $p \leq 0.001$), Cl^- and osmolality ($r = 0.802$, $p \leq 0.001$), Na^+ and osmolality ($r = 0.653$, $p \leq 0.001$), Cl^- and glucose ($r = 0.279$, $p \leq 0.050$), Na^+ and glucose ($r = -0.320$, $p \leq 0.030$), osmolality and glucose ($r = -0.279$, $p \leq 0.050$), hematocrit and protein ($r = 0.281$, $p = 0.039$), protein and cortisol ($r = 0.315$, $p \leq 0.020$), hematocrit and glucose ($r = 0.532$, $p = 0.001$), protein and glucose ($r = 0.350$, $p \leq 0.010$), and cortisol and glucose ($r = 0.270$, $p \leq 0.046$).

The increases in plasma cortisol and glucose conform to the general physiological stress response in fishes as described by Mazeaud et al. (1977) and the response to acid stress specifically (Lee et al. 1983; Brown et al. 1984, 1986; Barton et al. 1985). The loss of plasma Na^+ and Cl^-, the decrease in osmolality, and the increases in hematocrit, protein, and glucose all generally conform to past reports on the osmoregulatory and hematological responses to acidification (Packer and Dunson 1970, 1972; Neville 1979; Muniz and Leivestad 1980; McWilliams 1980; Booth et al. 1982; Lee et al. 1983; Giles et al. 1984; Barton et al. 1985; Brown et al. 1986).

The results support the conclusion that the physiological response to acidification is rapid. Other investigators have reported the same. Brown trout transferred from a neutral to a slightly acidic (pH 6.0) environment lost a significant amount of plasma Cl^- and Na^+ within 48 h (McWilliams 1980). This species also underwent a rapid change in hematocrit, but McWilliams, who used a milder pH, reported this to be a decrease, not an increase as found here. Booth et al. (1982) also measured a significant loss of plasma Cl^- in rainbow trout after 2 d of exposure to pH 4.0. Brook trout (*Salvelinus fontinalis*) exposed to lethal pH (<3.5) suffered a rapid loss of Na^+ (Packer and Dunson 1970, 1972). Death occurred within hours. Brown et al. (1984) found that rainbow trout exposed to pH 4.7 for 21 d showed continual increases in glucose and cortisol throughout the exposure and that significant differences from the controls could be seen as early as 4 and 8 d, respectively. These rates of increase are slower than those reported here for Arctic char. However, it should be remembered that the char, before being bled, had first been subjected to a behavioral test which in itself was stressful. The fact that the rainbow trout showed continual increases in these blood parameters is evidence that the rainbows experienced difficulty in adjusting to the acid. The Arctic char, on the other hand, were apparently able to compensate to some degree. This agrees with the mortalities suffered by the two groups. Brown et al. (1984) reported that the rainbows began dying after 18 d of exposure to pH 4.7 and that 33% of the group had died by the end of their 21-d exposure. In contrast, none of the Arctic char tested here died as a direct result of the acidification, nor were there any signs of impending mortality by the end of the 14-d exposure. This is in accordance with an earlier study (Jones et al. 1985a) where only one char died during a 19-d exposure to pH 4.5 Thus, it appears that rainbow trout are more sensitive to acid than are Arctic char. Giles et al. (1984) reported that rainbows would not be expected to survive at pH levels below 4.7.

During postexposure

The high cortisol level during postexposure was undoubtedly associated with the *Saprolegnia* infection. The stress of disease activates the pituitary–interrenal axis in fish, resulting in higher levels of circulating corticosteroids (Donaldson 1981; Pickering and Christie 1981). Conversely, high levels of cortisol seem to increase the susceptibility of salmonids to disease by inducing lymphocytopenia (Pickering and Duston 1983; Pickering 1984). Thus, the interrenal response itself may aggravate the situation even further.

Cortisol showed successive decreases over the next two test days but remained significantly higher than the controls after 2 wk of recovery. During postexposure, glucose continued to be correlated with hematocrit ($r = 0.548$, $p = 0.035$) and protein ($r = 0.636$, $p = 0.011$), but no correlation existed between hematocrit and protein. Cortisol was not significantly correlated with any of the other three parameters.

Blood hematocrit had also decreased to a level significantly lower than the controls 3 d after nonstressful conditions were restored. Normal hematocrit levels were later established by the end of the first week in clean water (Fig. 3A). Plasma protein and plasma glucose concentrations had returned to control levels after 3 d (Fig. 3B and C). Brown et al. (1986) reported similar results for rainbow trout.

Correlations between Physiological and Behavioral Parameters

No correlations were found at $p < 0.05$ between any physiological/behavioral pair in control fish (Table 1). With one exception (protein/attraction) the same was true for the postexposure group. When the control and postexposure groups were combined to make a larger sample, no significant correlations were found. In contrast, several physiological/behavioral combinations were significantly correlated in acid-stressed fish. Activity was correlated with protein and glucose, especially the latter. None of the blood parameters were related to thigmotaxis, but five parameters, particularly protein, were correlated with food extract attraction.

No single behavior could be explained purely in terms of linear changes in any one blood parameter. That is, no simple cause–effect relationship exists between any physiological/behavioral parametrical pair. Nevertheless, these relationships which could be expected to vary among individuals were significant in many cases. As evidenced by the lack of significant correlations within the control and postexposure groups, several relationships appear to hold only when the values of the blood parameters are elevated. Thus, conceivably there are critical thresholds below which behavior is relatively independent of minor fluctuations within these blood components. Applying this concept to, say, plasma glucose and food-searching behavior, one would expect that a positive orientation to chemical feeding cues would be unaffected by moderate rises and falls in blood sugar. However, when there are substantial elevations in plasma glucose, like those that occur after large meals or during stress, then one would expect food-searching behavior to be suppressed. This is the essence of the

TABLE 1. Correlations between three behavioral parameters and the seven blood parameters. The top value is the correlation coefficient; the bottom value (in parentheses) is the probability of exceeding the *F* statistic. *indicates significant values.

	Activity	Thigmotaxis	Attraction
Control (N = 16)			
Hematocrit	0.063	−0.225	−0.301
	(0.803)	(0.369)	(0.224)
Protein	0.234	−0.079	−0.272
	(0.350)	(0.755)	(0.275)
Cortisol	0.119	0.085	−0.272
	(0.639)	(0.737)	(0.538)
Glucose	0.045	0.139	0.049
	(0.861)	(0.583)	(0.848)
Exposure			
Cl^- (N = 45)	−0.156	0.040	0.275
	(0.195)	(0.582)	(0.056)
Na^+ (N = 42)	−0.072	0.100	0.200
	(0.448)	(0.330)	(0.141)
Osmolality (N = 36)	−0.155	0.018	0.108
	(0.263)	(0.379)	(0.379)
Hematocrit (N = 55)	−0.231	0.004	−0.318*
	(0.090)	(0.978)	(0.018)
Protein (N = 55)	−0.275*	0.128	−0.394
	(0.044)	(0.357)	(0.003)
Cortisol (N = 55)	−0.025	0.104	−0.310*
	(0.858)	(0.450)	(0.021)
Glucose (N = 55)	−0.359*	−0.031	−0.274*
	(0.007)	(0.821)	(0.043)
Postexposure (N = 15)			
Hematocrit	−0.044	0.084	−0.003
	(0.877)	(0.765)	(0.992)
Protein	0.245	0.069	0.515*
	(0.379)	(0.806)	(0.049)
Cortisol	0.211	−0.084	−0.118
	(0.449)	(0.766)	(0.676)
Glucose	0.198	−0.081	0.188
	(0.480)	(0.775)	(0.502)

glucostatic theory discussed by Fletcher (1984) in his review of the physiological control of appetite in fish and the possible role played by plasma metabolites.

The correlation between the blood parameters of stress and the accompanying behavior could prove useful in predicting the behavioral status of natural fish populations exposed to acid precipitation. Blood samples can be obtained from fish in the wild within moments of their capture. With the possible exception of cortisol which responds to stress within minutes, the levels of the various blood constituents in these samples can then be used to assess the degree of stress at the moment immediately prior to capture. The relative ease of these tests makes them attractive for such studies. In contrast, behavioral assays are generally tedious and time consuming to perform even in the controlled environment of the laboratory; the difficulties are magnified considerably when such tests are attempted in the field. Therefore, determining to what extent behavior might have been altered by an incidence of acid pollution or what proportion of a population is displaying stress behavior poses a serious problem for the behavioral ecologist. However, an indirect measure of these phenomena might be attained by estimating behavior from the levels of the plasma stress indicators measured on fish captured and sampled on location. The measure would, of course, only be relative. Nevertheless, much time and effort could be saved if any physiological/behavioral correlations were confirmed to hold true for fish in the field.

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References

ALMER, B., W. DICKSON, C. EDSTROM, E. HORNSTROM, AND U. MILLER. 1974. Effects of acidifications on Swedish lakes. Ambio 3: 30–36.

BARTON, B. A., G. S. WEINER, AND C. B. SHRECK. 1985. Effect of prior acid exposure on physiological responses of juvenile rainbow trout (*Salmo gairdneri*) to acute handling stress. Can. J. Fish. Aquat. Sci. 42: 710–717.

BEAMISH, R. J. 1972. Lethal pH for the white sucker *Catastomus commersoni* (Lacepede). Trans. Am. Fish. Soc. 101: 355–358.

BOOTH, J. H., G. F. JANSZ, AND G. F. HOLETON. 1982. Cl^-, K^+, and acid–base balance in rainbow trout during exposure to, and recovery from, sublethal environmental acidification. Can. J. Zool. 60: 1123–1130.

BROWN, S. B., J. G. EALES, R. E. EVANS, AND T. J. HARA. 1984. Interrenal, thyroidal, and carbohydrate responses of rainbow trout (*Salmo gairdneri*) to environmental acidification. Can. J. Fish. Aquat. Sci. 41: 36–45.

BROWN, S. B., R. E. EVANS, AND T. J. HARA. 1986. Interrenal, thyroidal, carbohydrate, and electrolyte responses in rainbow trout (*Salmo gairdneri*) during recovery from the effects of acidification. Can. J. Fish. Aquatic. Sci. 43: 714–718.

DAVIS, K. B., AND N. C. PARKER. 1983. Plasma corticosteroid and chloride dynamics in rainbow trout, Atlantic salmon, and lake trout during and after stress. Aquaculture 32: 189–194.

DAYE, P. G., AND E. T. GARSIDE. 1980. Structural alterations in embryos and alevins of the Atlantic salmon, *Salmo salar* L., induced by continuous or short-term exposure to acidic levels of pH. Can. J. Zool. 58: 27–43.

DIVELY, J. L., J. E. MUDGE, W. H. NEFF, AND A. ANTHONY. 1977. Blood PO_2, PCO_2, and pH changes in brook trout (*Salvelinus fontinalis*) exposed to sublethal levels of acidity. Comp. Biochem. Physiol. 57A: 347–351.

DONALDSON, E. M. 1981. The pituitary–interrenal axis as an indicator of stress in fish, p. 11–47. *In* A.D. Pickering [ed.] Stress and Fish. Academic Press, New York, NY.

ELLGAARD, E. G., AND J. Y. GILMORE III. 1985. Effects of different acids on the bluegill sunfish, *Lepomis machrochirus* Rafinesque. J. Fish. Biol. 25: 133–137.

EUROPEAN INLAND FISHERIES ADVISORY COMMISSION (EIFAC). 1969. Water quality criteria for European freshwater fish — extreme pH values and inland fisheries. Water. Res. 3: 593–611.

FALK, D. L., AND W. A. DUNSON. 1977. The effects of season and acute sublethal exposure on survival times of brook trout at low pH. Water Res. 11: 13–15.

FLETCHER, D. J. 1984. The physiological control of appetite in fish. Comp. Biochem. Physiol. 78A: 617–628.

FROMM, P. O. 1980. A review of some physiological and toxicological responses of freshwater fish to acid stress. Environ. Biol. Fishes 5: 79–93.

GILES, M. A., H. S. MAJEWSKI, AND B. HOBDEN. 1984. Osmoregulatory and hematological responses of rainbow trout (*Salmo gairdneri*) to extended environmental acidification. Can. J. Fish. Aquat. Sci. 41: 1686–1694.

GRAHAM, M. S., AND C. M. WOOD. 1981. Toxicity of environmental acid to the rainbow trout: interactions of water hardness, acid type, and exercise. Can. J. Zool. 59: 1518–1526.

HARA, T. J. 1976. Effects of pH on the olfactory responses to amino acids in rainbow trout, *Salmo gairdneri*. Comp. Biochem. Physiol. 54A: 37–39.

HARA, T. J., S. B. BROWN, AND R. E. EVANS. 1983. Pollutants and chemoreception in aquatic organisms, p. 248–306. *In* J. O. Nriagu [ed.] Aquatic toxicology. John Wiley & Sons, New York, NY.

HOGLUND, L.B. 1961. The reaction of fishes in concentration gradients. Fish. Board Swed. Inst. Freshwater Res. Drottningholm Rep. No. 43: 1–147.

JEFFRIES, D. S., C. M. COX, AND P. J. DILLON. 1979. Depression of pH in lakes and streams in central Ontario during snowmelt. J. Fish. Res. Board Can. 36: 640–646.

JOHNSON, D. W., AND D. A. WEBSTER. 1977. Avoidance of low pH in selection of spawning sites by brook trout (*Salvelinus fontinalis*). J. Fish. Res. Board Can. 34: 2215–2218.

JONES, K. A., T. J. HARA, AND E. SCHERER. 1985a. Behavioral modification in Arctic char (*Salvelinus alpinus*) chronically exposed to sublethal pH. Physiol. Zool. 58: 400–412.

1985b. Locomotor response by Arctic char (*Salvelinus alpinus*) to gradients of H^+ and CO_2. Physiol. Zool. 58: 413–420.

LEE, R. M., S. D. GERKING, AND B. JEZIERSKA. 1983. Electrolyte balance and energy mobilization in acid-stressed rainbow trout, *Salmo gairdneri*, and their relation to reproductive success. Environ. Biol. Fishes 8: 115–123.

LEIVESTAD, H., AND I. P. MUNIZ. 1976. Fish kill at low pH in a Norwegian river. Nature (Lond.) 259: 391–392.

LEMLY, A. D., AND R. J. F. SMITH. 1985. Effects of acute exposure to acidified water on the behavioral response of fathead minnow, *Pimephales promelas*, to chemical feeding stimuli. Aquat. Toxicol. 6: 25–36.

MACFARLANE, R. B., AND R. J. LIVINGSTON. 1983. Effects of acidified water on the locomotor behavior of the Gulf killifish, *Fundulus grandis*: a time series approach. Arch. Environ. Contam. Toxicol. 12: 163–168.

MAZEAUD, M. M., AND F. MAZEAUD. 1981. Adrenergic responses to stress in fish, p. 49–75. *In* A. D. Pickering [ed.] Stress and fish. Academic Press, New York, NY.

MAZEAUD, M. M., F. MAZEAUD, AND E.M. DONALDSON. 1977. Primary and secondary effects of stress in fish: some new data with a general review. Trans. Am. Fish. Soc. 106: 201–212.

MCWILLIAMS, P. G. 1980. Acclimation to an acid medium in the brown trout *Salmo trutta*. J. Exp. Biol. 88: 269–280.

MILLIGAN, L. C., AND C. M. WOOD. 1982. Disturbances in haematology, fluid volume distribution and circulatory function associated with low environmental pH in the rainbow trout, *Salmo gairdneri*. J. Exp. Biol. 99: 397–415.

MOUNT, D. I. 1973. Chronic effect of low pH on fathead minnow survival, growth, and reproduction. Water Res. 7: 987–983.

MUNIZ, I. P., AND H. LEIVESTAD. 1980. Acidification — effects on freshwater fish. *In* D. Drablos and A. Tollan [ed.] Proceedings of the International Conference on the Ecological Impact of Acid Precipitation. Acid Precipitation — Effects on Forest and Fish. SNSF-project, 1432 Aas, Norway.

NEVILLE, C. M. 1979. Sublethal effects of environmental acidification on rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 36: 84–87.

PACKER, R. K., AND W. A. DUNSON. 1970. Effects of low environmental pH on blood pH and sodium balance of brook trout. J. Exp. Zool. 174: 65–72.

1972. Anoxia and sodium loss associated with the death of brook trout at low pH. Comp. Biochem. Physiol. 41: 17–26.

PETERSON, R. H., AND D. J. MARTIN-ROBICHAUD. 1983. Embryo movements of Atlantic salmon (*Salmo salar*) as influenced by pH, temperature, and state of development. Can. J. Fish. Aquat. Sci. 40: 777–782.

PICKERING, A. D. 1984. Cortisol-induced lymphocytopenia in brown trout, *Salmo trutta* L. Gen. Comp. Endocrinol. 53: 252–259.

PICKERING, A. D., AND P. CHRISTIE. 1981. Changes in the concentration of plasma cortisol and thyroxine during sexual maturation of the hatchery-reared brown trout, *Salmo trutta* L. Gen. Comp. Endocrinol. 44: 487–496.

PICKERING, A. D., AND J. DUSTON. 1983. Administration of cortisol to brown trout, *Salmo trutta* L., and its effects on the susceptibility to *Saprolegnia* infection and furunculosis. J. Fish Biol. 23: 163–176.

RAHEL, F. J., AND J. J. MAGNUSON. 1983. Low pH and the absence of fish species in naturally acidic Wisconsin lakes: inferences for cultural acidification. Can. J. Fish. Aquat. Sci. 40: 3–9.

SOIVIO, A., AND M. NIKINMAA. 1981. The swelling of erthrocytes in relation to the oxygen affinity of the blood of the rainbow trout, *Salmo gairdneri*, p. 101–119. *In* A. D. Pickering [ed.] Stress and fish. Academic Press, New York, NY.

SOMERS, K. M., AND H. H. HARVEY. 1984. Alteration of fish communities in lakes stressed by acid deposition and heavy metals near Wawa, Ontario. Can. J. Fish. Aquat. Sci. 41: 20–29.

SPRAGUE, J. B. 1969. Measurement of pollutant toxicity to fish. I. Bioassay method for acute toxicity. Water Res. 3: 793–821.

STRANGE, R. J., C. B. SHRECK, AND J. T. GOLDEN. 1977. Corticoid stress responses to handling and temperature in salmonids. Trans. Am. Fish. Soc. 106: 213–218.

SWARTS, F. A., W. A. DUNSON, AND J. E. WRIGHT. 1978. Genetic and environmental factors involved in increased resistance of brook trout to sulfuric acid solutions and mine acid polluted waters. Trans. Am. Fish. Soc. 107: 651–677.

WEDEMEYER, G. A., AND D. J. MCLEAY. 1981. Methods for determining the tolerance of fishes to environmental stressors, p. 247–275. *In* A. D. Pickering [ed.] Stress and fish. Academic Press, New York, NY.

Improved Estimation of the Dry Weight of *Holopedium gibberum* (Crustacea, Cladocera) Using Clutch Size, a Body Fat Index, and Lake Water Total Phosphorus Concentration

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Holopedium gibberum is one of the most important species of crustacean zooplankton in Canadian Shield lakes, yet satisfactory length–weight relationships (LWR's) have not been constructed from North American populations. In this report we show that, despite assertions to the contrary, weights of individual *H. gibberum* can be successfully predicted from body length (L) of animals measured in a nonanaesthetized, relaxed position. We use a relationship between postabdomen length and L to show that LWR's of Ontario and Scandinavian populations of *H. gibberum* differ. As such differences among lakes are the rule and not the exception, it is not safe to assume that published LWR's for zooplankton are widely applicable. Consideration of clutch size (CS) and a body fat index (BFI) in addition to L significantly improved estimates of the dry weight of *Holopedium* from Plastic Lake in central Ontario. This model provided more accurate estimates of *Holopedium* dry weight in 29 test lakes than the simple LWR, i.e. it had wider applicability. Predicted weights in the test lakes were further improved by consideration of lake water total phosphorus concentrations.

Holopedium gibberum est une des plus importantes espèces de crustacés zooplanctoniques présents dans les lacs du bouclier canadien; cependant, des relations longueur–poids satisfaisantes n'ont pas encore été élaborées pour les populations nord-américaines. Dans le présent rapport, les auteurs montrent que, malgré des airs contraires, le poids de chaque *H. gibberum* peut être prédit avec succès à partir de la longueur du corps (L) des individus non anesthésiés mesurés en position relâchée. Les auteurs utilisent une relation entre la longueur postabdominale et L pour montrer que les relations longueur–poids chez les populations de l'Ontario et de la Scandinavie sont différentes. Comme de telles différences entre les lacs sont la règle plutôt que l'exception, il n'est pas prudent de supposer que les relations longueur–poids relevées dans les ouvrages publiés sur le zooplancton sont généralement applicables. L'utilisation de la taille de la masse d'œufs et d'un indice de la teneur en graisse corporelle, en plus de L, améliore nettement les estimations du poids sec de *Holopedium* présent dans le lac Plastic, au centre de l'Ontario. Ce modèle a fourni des estimations plus précises du poids sec de *Holopedium* dans 29 lacs expérimentaux par rapport à la simple relation longueur–poids, c'est-à-dire que le modèle avait une application plus large. Des prévisions des poids dans les lacs expérimentaux étaient davantage améliorées quand les concentrations lacustres de phosphore total étaient considérées.

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Students of zooplankton ecology often require estimates of the biomass of zooplankton communities. This parameter is seldom determined directly; rather, it is usually estimated as the product of the numerical density and individual weights of the organisms of interest. Individual weights in turn are often estimated from length (usually body length) – weight relationships (LWR's). A large number of LWR's have been developed (Dumont et al. 1975; Bottrell et al. 1976; Rosen 1981; McCauley 1984; Culver et al. 1985); but, where they have been compared, model parameters for individual species often differ among lakes (Culver et al. 1985; Tessier 1986). Such models, therefore, may not be widely applicable.

Models that, in addition to length, include indices of physiological condition and environmental covariates that influence animal weight should have much wider applicability. For

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example, consideration of clutch size (eggs or embryos per individual) is known to improve predictions of zooplankton weight (Geller and Müller 1985). The fat content of individual Cladocera is readily estimable (Tessier and Goulden 1982) and should also improve predictions of cladoceran weights, although this has not been demonstrated as yet. Predictions of weight might also be improved by consideration of zooplankton food supply (Geller and Müller 1985), or its correlate, lake water nutrient levels. Carter et al. (1983) felt that the positive relationship between body length of the copepod *Diaptomus minutus* and water colour they observed for lakes in eastern North America might be related to decreased vulnerability of diaptomids to visually cued predatory fish in more coloured waters. As height to length ratios can vary substantially for zooplankton (Sládaček 1950), and as visibility should be a function of both height and length, consideration of water colour might also improve predictions of zooplankton weight, since dry weight is probably a better correlate of visibility than is length alone. Finally, as many Precambrian Shield lakes have been influenced by acidic precipitation (Dillon et al. 1979), and as Roff and Kwiatkowski (1977) reported smaller dry weights of a cladoceran zooplankter in acidic than in nonacidic lakes, consideration of lake alkalinity might improve predictions of zooplankton dry weights in such lakes.

In this report a LWR is developed for *Holopedium gibberum* Zaddach from Plastic Lake, a nutrient-poor, softwater lake in central Ontario, Canada. We compare this LWR with published models to see if the anticipated difference occurs, and determine if consideration of clutch size (CS) and a body fat index (BFI, equivalent to the sum of Tessier and Goulden's lipid and ovarian indices) improves estimates of the dry weight of *H. gibberum*. We then determine whether Plastic Lake models including CS and BFI produce more accurate estimates of *H. gibberum* dry weights in 29 test lakes than the simple LWR. Finally, we determine if the estimates are further improved by consideration of the water colour, total phosphorus (TP) concentration, and alkalinity of the test lakes.

Holopedium gibberum was selected as the test organism because it is one of the most frequently encountered cladoceran species in temperate lakes (Carter et al. 1980) and because there are procedural and predictive weaknesses in published LWR's for the species. Linear relationships between length and weight, such as those reported by Ferrante (1976) and Makarewicz and Liken (1979), are suspect on the basis of general allometric principles (Peters 1983). As Bottrell et al. (1976) used a very small data set ($n = 8$), the robustness of their LWR may be poor. Finally, models such as that of Persson and Ekbohm (1980), which depend on measurement of postabdominal length, are difficult to use in practice, especially when large numbers of animals must be examined on a routine basis.

Methods

Description of the Study Lakes and Sampling Methods

Plastic Lake (45°11'N, 78°50'W) has an area of 32.3 ha and a mean and maximum depth of 8.0 and 16.0 m, respectively. In 1985 the lake had a spring TP level of 6μg/L and a mean Secchi transparency of 7.6 m (P. J. Dillon, unpubl. data). *Holopedium gibberum* was the largest contributor to average zooplankton biomass in the lake (N. D. Yan, unpubl. data).

The 29 test lakes were located on the Canadian Shield in south-central Ontario. For these lakes, water colour averaged 33.2 Hazen units, TP 8.7μg/L, and total inflection point alkalinity (ALK-TIP) 6.88 mg/L as $CaCO_3$. The values of the parameters ranged from <1 to 135 Hazen units, 2 to 22.5 μg/L, and −1.1 to 59.8 mg/L, respectively. ALK-TIP was not correlated with TP ($r = 0.08$, $P > 0.10$) or with colour ($r = 0.20$, $P > 0.10$) for these 29 lakes, but water colour and TP were positively correlated ($r = 0.90$, $P < 0.01$).

We visited Plastic Lake at biweekly intervals during the ice-free season of 1985 and the test lakes on a single occasion between June 1 and September 30, 1985. *Holopedium gibberum* was collected at the deepest spot in Plastic Lake and at a deep spot in each of the test lakes in one to six vertical hauls from 2 m above the bottom or three times the Secchi transparency (whichever was shallower) to the lake surface, using a 0.75-m-diameter, 2-m-long conical tow net constructed of 250-μm nylon mesh. The animals were returned to the laboratory in Dorset, Ontario, in clean, opaque plastic containers filled with lake water. They were processed within 4 h for Plastic Lake and within 24 h for all test lakes. Samples were refrigerated until processing if the time between collection and processing exceeded 1 h.

Water samples used for colour and ALK-TIP determination were pumped from the middle of the epilimnion and analyzed according to Ontario Ministry of the Environment (1981). We did not collect samples for phosphorus analysis. M. Stephenson (Department of Zoology, University of Guelph) kindly provided surface (0.5 m) water TP levels collected from each lake during the ice-free season of 1984. These samples had been analysed using an autoclave digestion procedure found to be suitable for such waters (Jeffries et al. 1979).

Measurement Methods

Unlike other Cladocera, *H. gibberum* does not possess a rigid carapace. In consequence, Bottrell et al. (1976), Persson and Ekbohm (1980), and Johansson and Olofsson (1976, cited in Persson and Ekbohm 1980) used the presumably constant length of each animal's postabdomen as the predictor variable in development of LWR's. In terms of microscope manipulations, there are logistic advantages to a *carapace* length-body weight model, especially where measurements of hundreds of individuals are desired. Therefore, we decided to use carapace length of nonanaesthetized animals to develop our models.

In the laboratory, we observed that *H. gibberum* alternated among three positions in terms of the degree of long-axis flexure-extended, relaxed, and contracted, the last being the position normally illustrated in texts and observed in preserved specimens. The dorsal margin of the carapace develops a large ventrally directed crimp when animals are in the extended position. In the relaxed postion (Fig. 1), the crimp disappears. The dorsal surface of the postabdomen and the posterior half of the dorsal edge of the carapace lie in a smooth curve interrupted only by the base of the setae natatores which is positioned just behind the posterior tip of the carapace. We measured carapace lengths (L) of individuals that were in the relaxed position.

To measure the animals, we first concentrated the samples by gentle (i.e. submerged) filtration through 1000-μm mesh and then dispensed the concentrate into a shallow petrie dish with very little or often no added water. Using this technique the *H. gibberum* were effectively immobilized by their hyaline gelatinous capsules on the base of the dish. An image of the animal of interest was displayed by a microscope-mounted

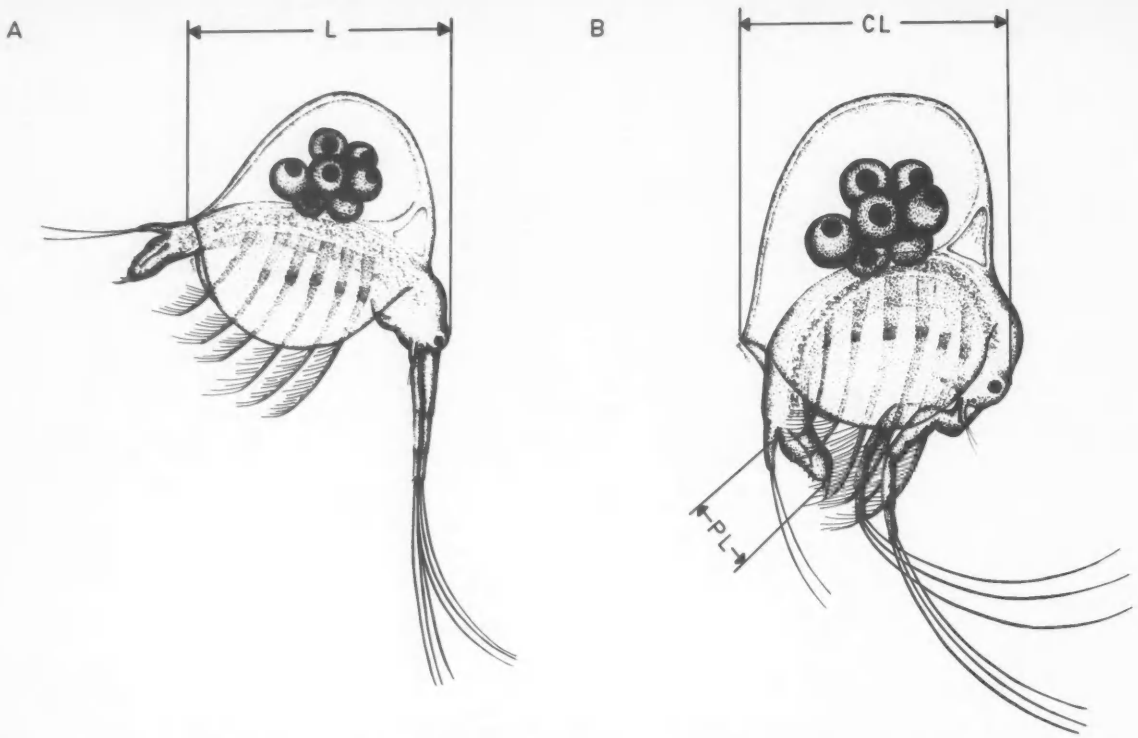

FIG. 1. Sketch of *H. gibberum* in (A) relaxed and (B) contracted positions. CL, L, and PL indicate measurements taken for contracted and relaxed carapace lengths and postabdomen length, respectively.

video camera on a high-resolution colour monitor, and the carapace length was determined using electronic calipers identical to those descibed by Sprules et al. (1981). The standard error of replicate measurements (n = 20) was 0.2% of the mean length. We scored the BFI following Tessier and Goulden (1982) and CS of the selected individual and then placed it on a small preweighed (±0.5 μg) teflon strip. Unlike in Persson and Ekbohm (1980), the capsules were included in the analysis. Histochemically, the capsule resembles a nonmineralized carapace (Brown 1970). Separate analyses of capsule weights of large animals suggested that they form ~5% of total body weight. Capsule weights are proportionately more important for small animals (Tessier 1986).

Animals were dried to constant weight (reached within 1 h) at 60 ± 2°C and then held over silica gel prior to weighing to the nearest microgram on a Cahn model 29 electrobalance. We were forced to pool animals of similar length, CS, BFI, and stage of development of embryos (where applicable) to determine weights accurately. The number of animals pooled averaged 7.5 per determination and decreased with animal size. The mean (± 1 SD) weight of composites was 100 ± 65 μg for Plastic Lake collections and 137 ± 55 μg for collections from the test lakes.

We used a different protocol to select animals in Plastic Lake and in the test lakes. For Plastic Lake, we dried animals which represented the range of sizes and fecundities of *Holopedium* existing on each date from May 15, when they first appeared in the samples in abundance, to September 5, when densities fell to undetectable levels (<0.01·L^{-1}). As we visited each of the test lakes on only a single occasion, we picked animals most representative of the predominant body and clutch sizes present at the time.

A total of 665 animals were selected from Plastic Lake and 1043 from the test lakes. After formation of composites, these produced 93 sets of data from Plastic Lake and 134 from the test lakes.

Holopedium contract upon preservation. We developed a relationship between contracted (CL) and relaxed (L) carapace lengths (Fig. 2) because LWR's using CL as a predictor variable would be of more interest to potential users. Forty animals ranging widely in length (Fig. 2) were selected from the June 28 collections from Plastic Lake. We measured carapace lengths in the relaxed position than individually preserved and maintained the animals in chilled 3% sugar-formalin. The carapace lengths were remeasured after 5 and 240 h of preservation, but no contraction was noted after 5 h.

Data Analyses

The length-weight data displayed the anticipated heteroscedasticity (Fig. 3). This was successfully eliminated by natural log transformation. Using an HP 9845B computer, we constructed a variety of regression models from the Plastic Lake collections with individual weight (ln W) of *H. gibberum* as the dependent variable. Two models were produced with carapace length (ln L) as the single predictor variable. The first used all the data (n = 93); the second used data from the 58 nongravid animals. The distribution of residuals was normal

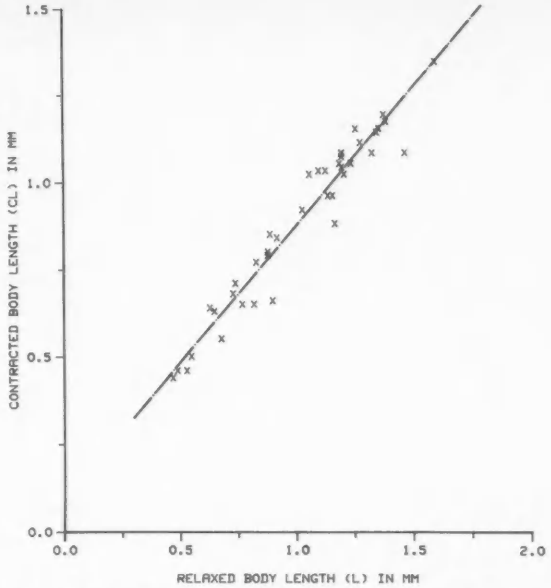

FIG. 2. Relationship between carapace length of preserved (contracted position CL) and live (relaxed position L) specimens of *H. gibberum* for Plastic Lake. The regression equation for the indicated line is CL = 0.781L + 0.0912 (r^2 = 0.94, RMS = 0.0034, P <0.01).

for the second model, while it was slightly skewed by inclusion of gravid animals in the first model. We developed a third model using ln L and CS as predictors, two variables that are theoretically estimable in archived samples. Finally, we ran a stepwise linear regression analysis on the Plastic Lake data with a predictor variable matrix including ln L, CS and BFI. Residuals were normally distributed for the third and fourth models. The analyses were then repeated replacing ln L with ln CL calculated using the equation given in the caption to Fig. 2.

To test the general usefulness of the Plastic Lake models, we regressed *H. gibberum* weights observed in the test lake set against the weights predicted from the models developed using relaxed carapace lengths. We compared the magnitude of the coefficients of determination of the regressions and the divergence of the slopes from unity and the intercepts from zero. Finally, we ran two stepwise regression analyses on the test data set using first ln L, then ln CL, and BFI, CS, TP, colour, and ALK-TIP as predictor variables. For all stepwise regression analyses, the decision criterion for inclusion or deletion of variables in the developing model was a partial F statistic > F-to-enter (P = 0.05) and an increase in multiple correlation coefficient upon inclusion of the variable of ≥0.01.

Results and Discussion

Model Development

Summary statistics of the four attributes of *H. gibberum* in the two data sets are presented in Table 1. There is substantial overlap between the data sets for all variables, although we did select more small animals in Plastic Lake.

The range in CS is not unusual for the species. Larsson (1978), for example, observed a mean CS of up to 10 eggs per egg-bearing female in (Lake) Ovre Heimdalsvatn. The maximum value observed was 21 per female, a value similar to that of the Plastic Lake population. The upper body size limit of 2.2 mm is larger than observed in other studies (Stenson 1973; Larsson 1978; Makarewicz and Likens 1979), but this is undoubtedly a methodological artifact attributable to our use of live rather than preserved, i.e. contracted, specimens.

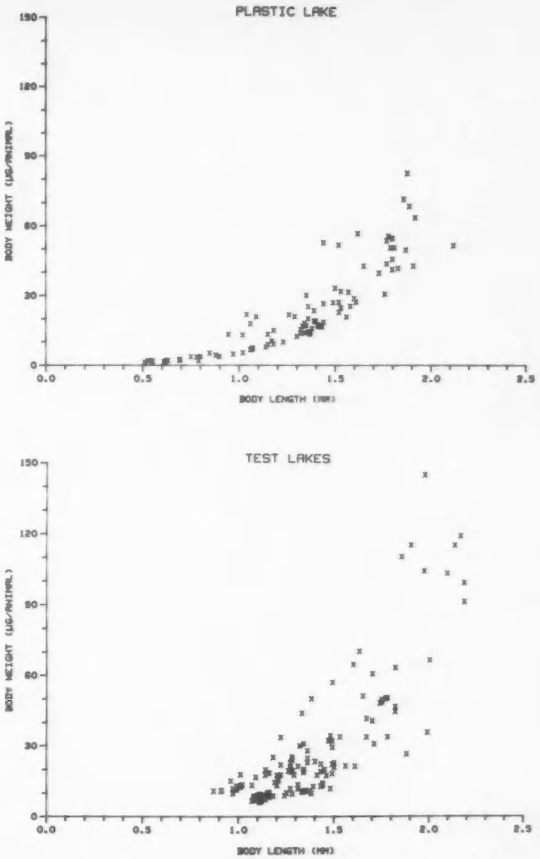

FIG. 3. Scattergram of *H. gibberum* body length – body weight data from Plastic Lake (n = 93) and the test lake set (n = 134).

TABLE 1. Summary statistics of *H. gibberum* dry weight (W in µg/animal), body length (L in mm), clutch size (CS in eggs or embryos/animal), and body fat index (BFI) for Plastic Lake and the test lake set. There were no missing values in the data matrices.

Parameter	Arithmetic mean	SD	Range
Plastic Lake (n = 93)			
W	23.9	19.1	1.45–83.0
L	1.33	0.38	0.51–2.12
CS	1.59	3.25	0–22
BFI	0.39	0.73	0–3
Test lakes (n = 134)			
W	27.9	27.3	6.2–146.0
L	1.37	0.09	0.87–2.18
CS	1.35	2.21	0–10
BFI	0.52	0.90	0–3

TABLE 2. Models produced by the regression analyses on data from the Plastic Lake *H. gibberum*. Variable names are given in Table 1. Values of r_i^2 are incremented to show the change in r^2 upon addition of the ith variable to the model. The regression residual mean square (RMS) and F statistic are indicated. Models 2 and 6 are for nongravid animals only; the remaining models are for gravid and nongravid animals.

No.	Model[a]	r_1^2	r_2^2	r_3^2	RMS	F	n
	Using L						
1	ln W = 2.96 ln L + 2.07	0.91			0.10	902	93
2	ln W = 2.86 ln L + 1.95	0.95			0.057	1078	58
3	ln W = 2.82 ln L + 0.0631CS + 2.00	0.91	0.94		0.062	763	93
4	ln W = 2.80 ln L + 0.203BFI + 0.0467CS + 1.96	0.91	0.94	0.96	0.044	739	93
	Using CL						
5	ln W = 3.30 ln CL + 2.50	0.91			0.10	924	93
6	ln W = 3.21 ln CL + 2.36	0.96			0.051	1211	58
7	ln W = 3.14 ln CL + 0.0629CS + 2.41	0.91	0.95		0.061	791	93
8	ln W = 3.12 ln CL + 0.207BFI + 0.0456CS + 2.36	0.91	0.95	0.96	0.041	792	93

[a]Range in L was 0.51–1.88 mm for model 2 and 0.51–2.12 mm for models 1, 3, and 4.

TABLE 3. Comparison of regressions of weight as a function of postabdomen length (PL in μm). RMS and other regression diagnostics are provided where available. For the Plastic Lake model, PL was calculated from measured carapace lengths (L) using PL = 191.64L + 37.0.

Model	n	r^2	RMS	Source[a]
ln W = 3.19 ln PL − 15.54	142	0.87	0.201	Persson and Ekbohm 1980
ln W = 3.052 ln PL − 14.82	107	0.94	—	Johansson and Olafsson 1976 (cited in Persson and Ekbohm 1980)
ln W = 2.056 ln PL − 8.8	8	0.97	0.058	Larsson 1978; Bottrell et al. 1976
ln W = 3.52 ln PL − 17.08	93	0.91	0.099	This study

[a]Developed for lakes in the Kuokkel area, Kloten area, and (Lake) Ovre Heimdalsvatn in Sweden and from Plastic Lake, respectively.

Models produced by the regression analyses of the Plastic Lake data are listed in Table 2. It is clear that relaxed body length is a useful predictor of *H. gibberum* dry weight. The residual mean square of Persson and Ekbohm's (1980) postabdomen length–body weight model was 0.20, greater than in both univariate models developed for the Plastic Lake population (numbers 1 and 2 in Table 2). Of these two models, number 2 is clearly the superior model for nongravid animals in Plastic Lake.

As CS is measurable in archived samples, we included it with ln L in the first stepwise regression analysis, and it did improve predictability of ln W (model 3). However, CS was replaced as the second predictor by BFI, in the next analyses where ln L, BFI, and CS were included as predictor variables (model 4 in Table 2). To our knowledge, this is the first time an index of body fat has been included in a model that may be used to predict the dry weight of a zooplankter. This extends the usefulness of Tessier and Goulden's indices.

The regression models developed using calculated CL rather than L (numbers 5–8 in Table 2) closely resembled those using relaxed length, although parameter estimates for CL were somewhat larger, as expected. The actual uncertainty of predictions of *H. gibberum* dry weight using equations 5–8 would, of course, be greater than indicated by the regression residual mean squares alone, as the uncertainty of the CL–L model would have to be considered (see Fig. 2). However, use of the CL–L model does not bias predictions.

Comparison with Other LWR's

Excluding the LWR's of Ferrante (1976) and Makarewicz and Likens (1979), there are three published LWR's for *H. gibberum* (Table 3). All use as a predictor variable the length of the animal's postabdomen measured from the base of the terminal postabdominal claw to the base of the setae natatores. To compare our data with published models, we first constructed a postabdomen length – body length relationship.

We measured body lengths (L in millimetres) and postabdomen lengths (PL in micrometres, Fig. 1) of 46 *H. gibberum* collected in May 1985 from Plastic Lake and from three of the test lakes, Heney, Dickie, and Blue Chalk (the three test lakes were added to increase the size range of animals). The following relationship, illustrated in Fig. 4, was developed:

$$(1)\quad PL = 191.64\ L + 37.00 \quad (r^2 = 0.88,\ P < 0.01).$$

Using equation 1, we then estimated PL from L for the entire Plastic Lake data set and calculated a new LWR (Table 3) using PL as the predictor variable. As the parameters of the three published regression equations fell outside the 95% confidence intervals about both the slope (3.29 to 3.75) and the intercept (−18.37 to −15.78) of the Plastic Lake LWR, we concluded that the Plastic Lake LWR differed from the published models. Weights predicted from the Plastic Lake model exceed predictions of the other three models for PL's greater than about 290 μm.

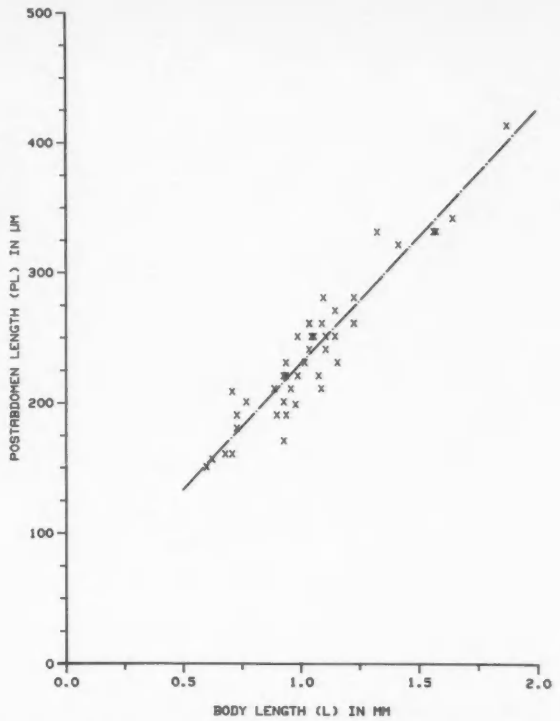

FIG. 4. Relationship between postabdomen length (PL) and relaxed carapace length (L) of *H. gibberum* taken from Plastic, Dickie, Heney, and Blue Chalk lakes in late May 1985. The regression equation is illustrated. Regression diagnostics are presented in text.

We do not intend to explore this difference among the models for three reasons. First, as previously indicated, differences between LWR's for a single species in different water bodies are the norm, not the exception (Culver et al. 1985); hence, it was not a surprising observation. Second, the Plastic Lake LWR was developed from calculated and not measured PL. Therefore, model predictions suffer from a source of uncertainty that the three Swedish models do not possess. Finally, the analyses of Plastic Lake data indicate that *H. gibberum* dry weights are influenced by CS and body fat. Possession of these data might explain the differences between the models, but these data were not available for the published LWR's.

Model Testing

The model developed from the nongravid Plastic Lake animals (equation 2 in Table 2) was a poor predictor of ln W of nongravid *H. gibberum* in the test lakes (Table 4). Observed values exceeded predicted values for the largest animals in particular (Fig. 5B). The six nongravid animals weighing > 100 μg (ln W > 4.6, Fig. 5B) in the test data set all had a BFI of 3. In the Plastic Lake data set, in contrast, only 1 of the 58 nongravid animals had a BFI of 3, the next largest being 1.1. In comparison with the test data set, large, lipid-rich animals were therefore under-represented in the data set used for model development. The model's performance was poor as a result.

In contrast, the three models (numbers 1, 3, and 4 in Table 2) developed from the entire Plastic Lake data set (gravid + nongravid animals) were all successful predictors of the natural log of *H. gibberum* dry weight in the test lakes. The slopes of the regression equations of predicted versus observed weights did not deviate significantly from unity (e.g. Fig. 5A), nor the intercepts from zero (Table 4). A comparison of the coefficients of determination of these three models indicated that consideration of CS and body fat improved the accuracy of estimates of *H. gibberum* dry weight in comparison with the predictions of the simple LWR.

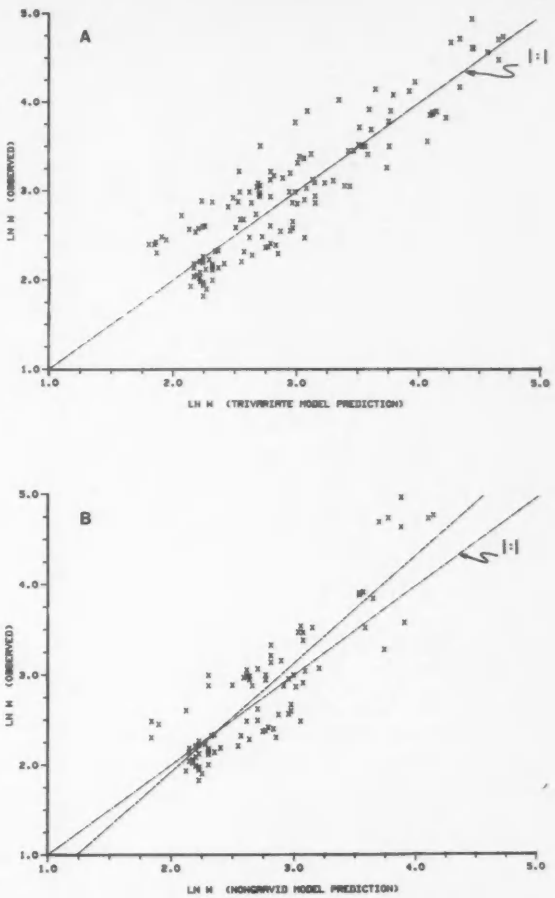

FIG. 5. Comparison of measured body weight (ln W) of *H. gibberum* for the test lakes with that predicted from (A) equation 4 in Table 2, the model predicting in W from ln L, BFI, and CS, and (B) equation 2 in Table 2, the univariate model for nongravid animals. The 1:1 lines are indicated. Regression diagnostics of observed versus predicted ln W are presented in Table 4. In Fig. 5B, the second line represents the regression equation of observed on measured weights.

Phosphorus, Colour, and Alkalinity

The stepwise regression analysis run on the test lake data produced the following model:

$$(2)\quad \ln W = 2.310 \ln L + 0.1186CS + 0.3487BFI + 0.0305TP + 1.7122.$$

Predictor variables entered the model in the indicated order and

TABLE 4. Summary of the comparison of measured weights for the test lake animals with those predicted using models developed from Plastic Lake *H. gibberum* data. The indicated slopes and intercepts (±95% confidence limits) and RMS, r^2, and n are the parameters and regression diagnostics of a linear regression equation of observed ln W of *H. gibberum* in the test lake set on ln W predicted from the indicated models. An asterisk indicates a significant deviation of the slope from unity or the intercept from zero ($P = 0.05$). The models used are presented in Table 2. Data for gravid animals were deleted from the test set prior to the evaluation of model 2, the model developed using nongravid animals only.

Model tested						
No.	Description	Slope	Intercept	RMS	r^2	n
1	ln L	1.02 ±0.115	0.01 ±0.346	0.175	0.70	134
2	ln L	1.21 ±0.144*	−0.497±0.402*	0.134	0.76	87
3	ln L, CS	1.07 ±0.100	−0.122±0.297	0.132	0.77	134
4	ln L, BFI, CS	0.945±0.067	0.220±0.237	0.109	0.81	134

the multiple r^2 increased from 0.70 to 0.78 to 0.88 to 0.92, while the regression residual mean square fell from 0.175 to 0.127 to 0.069 to 0.048, respectively. The partial F was significant ($P = 0.05$) for inclusion of ALK-TIP at the fifth iteration of the analysis, but we did not include it in the model, as the increase in multiple r^2 would have been <0.01.

Replacing ln L with ln CL and rerunning the analyses produced the following very similar model with virtually identical regression diagnostics:

$$(3)\quad \ln W = 2.510 \ln CL + 0.118CS + 0.346BFI + 0.0304TP + 2.063.$$

Usefulness of TP, CS, and BFI

While TP was the last variable to enter equation 2, its influence on predicted *H. gibberum* weight can be dramatic. For example, the predicted weight of a nongravid 1.0-mm-long animal with a BFI of zero would increase by 86%, from 5.9 to 11 μg, if lake water TP increased from 2 to 22.5 mg/m^3, the range observed in the test lake data set. Differences in trophic status among lakes may be an additional partial explanation for the differences in LWR's observed by Culver et al. (1985) for individual species.

As the analysis provides correlational and not causal information, we must guess why TP improves the predictability of ln W over that possible using ln L, BFI, and CS alone. The interpretation is further complicated by the significant relationship between colour and TP among the test lakes ($r = 0.90$, $P < 0.01$). While picking the animals for determination of dry weight, we did observe that those animals found in the nutrient-rich and coloured lakes were particularly tall (and presumably heavy) for their length. In laboratory studies, Sládeček (1950) observed a wide range in heights for *H. gibberum* of particular lengths. As both body height and length could influence the vulnerability of animals to visually cued predatory fish, the "visibility" hypothesis of Carter et al. (1983) mentioned in the introduction may explain the inclusion of TP in the model. Alternatively, its inclusion may have a direct explanation. Exclusive of fat content and CS, the weight to length ratio of *H. gibberum* may increase in richer waters simply because of the abundance of food.

Explicit consideration of CS and BFI in addition to L should allow more accurate estimates of seasonal changes in *H. gibberum* mean weight than possible using LWR's alone. For example, Larsson (1978) noted that the mean CS of gravid *Holopedium* in Ovre Heimdalsvatn ranged from 1 to 10 over the growing season. Ignoring the small bias produced by detransformation of ln W (Bird and Prairie 1985), equation 4 in Table 2 indicates that an increase in CS of 1−10 eggs per female would produce a 53% increase in the estimated dry weight of an animal with a BFI of zero. As seasonal changes in CS may certainly be as large as this for other Cladocera (e.g. Murtaugh 1985), and as consideration of CS improves estimates of dry weight for other Cladocera (Geller and Müller 1985), it is clear that investigators requiring accurate estimates of seasonal changes in cladoceran biomass should consider the use of models that include CS. Fecundity, of course, varies between lakes as well; hence, models including CS should have wider applicability (e.g. Table 4) than simple LWR's.

Like CS, the lipid content of Cladocera varies over the growing season. For example, Tessier and Goulden (1982) and Tessier (1984) reported that mean values of BFI of *Holopedium* and *Daphnia* in three lakes in the northeastern United States varied from 0 to 2 over a growing season. Using equation 4 in Table 2, an incrase in BFI from 0 to 2 would produce a 50% increase (7.06−10.6μg) in the estimated mean weight of 1.0-mm nongravid *Holopedium*. Clearly, consideration of changes in BFI could significantly improve estimates of seasonal changes in zooplankton biomass in situations where BFI varies over time.

Tessier and Goulden (1982) noted that samples must be refrigerated after preservation and examined within 2 d if BFI is to be estimated. This presents a serious logistic limitation to the usefulness of body fat indices for improving estimates of cladoceran dry weight, but the problem might be resolvable by novel approaches to sample processing. For example, while it might not be possible to enumerate samples within 48 h of collection, it might be possible to prepare colour videocassette recordings of samples for later enumeration.[2]

In the last few years the falling cost of microcomputers has encouraged the partial automation of the enumeration of zooplankton samples (Sprules et al. 1981; Mills and Confer 1986). It would not be difficult to log clutch size and body fat indices along with the length and identity of enumerated animals using such systems. Depending on the investigator's questions, improvements in estimates of zooplankton biomass that would result might well justify the time spent in developing associated computer software and in extending the models pre-

[2]FOOTNOTE ADDED IN PROOF: The use of lipophilic dyes may solve the sample storage problem (B. Bjorkman and J. Shapiro. 1986. Measurement of the lipid ovary index on stored zooplankton samples. Limnol. Oceanogr. 31: 1138−1139).

sented herein to other Cladocera and to more nutrient-rich systems.

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References

Bird, D. F., and Y. T. Praire. 1985. Practical guidelines for the use of zooplankton length–weight regression equations. J. Plankton Res. 7: 955–960.

Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbright-Ilkowska, H. Kurasawa, P. Larsson, and T. Weglenska. 1976. A review of some problems in zooplankton production studies. Norw. J. Zool. 24: 419–456.

Brown, S. C. 1970. Histochemical studies on the hyaline capsule of *Holopedium gibberum* Zaddach (Crustacea, Cladocera). Histochemie 21: 160–169.

Carter, J. C. H., M. J. Dadswell, J. C. Roff, and W. G. Sprules. 1980. Distribution and zoogeography of planktonic crustaceans and dipterans in glaciated eastern North America. Can. J. Zool. 58: 1355–1387.

Carter, J. C. H., W. G. Sprules, M. J. Dadswell, and J. C. Roff. 1983. Factors governing geographical variation in body size of *Diaptomus minutus* (Copepoda, Calanoida). Can. J. Fish. Aquat. Sci. 40: 1303–1307.

Culver, D. A., M. M. Boucherle, D. J. Bean, and J. W. Fletcher. 1985. Biomass of freshwater crustacean zooplankton from length–weight regressions. Can. J. Fish. Aquat. Sci. 42: 1380–1390.

Dillon, P. J., N. D. Yan, W. A. Scheider, and N. Conroy. 1979. Acidic lakes in Ontario, Canada: characterization, extent and responses to base and nutrient additions. Arch. Hydrobiol. Beih. Ergebn. Limnol. 13: 317–336.

Dumont, H. J., I. Van De Velde, and S. Dumont. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda, and Rotifera from the plankton, periphyton, and benthos of continental waters. Oecologia (Berl.) 19: 75–97.

Ferrante, J. G. 1976. The role of zooplankton in the intrabiocoenotic phosphorus cycle and factors affecting phosphorus excretion in a lake. Hydrobiologia 49: 203–214.

Geller, W., and H. Müller. 1985. Seasonal variability in the relationship between body length and individual dry weight as related to food abundance and clutch size in two coexisting *Daphnia* species. J. Plankton Res. 7: 1–18.

Jeffries, D. S., F. P. Dieken, and D. E. Jones. 1979. Performance of the autoclave digestion method for total phosphorus analysis. Water Res. 13: 275–279.

Larsson, P. 1978. The life cycle dynamics and production of zooplankton in Ovre Heimdalsvaton. Holarct. Ecol. 1: 162–218.

Makarewicz, J. C., and G. E. Likens. 1979. Structure and function of the zooplankton community of Mirror Lake, New Hampshire, Ecol. Monogr. 49: 109–127.

McCauley, E. 1984. The estimation of the abundance and biomass of zooplankton in samples, p. 228–265 *In* J. A. Downing and F. H. Rigler [ed.] A manual on methods for the assessment of secondary productivity in fresh waters. 2nd ed. Blackwell Scientific Publications, Oxford.

Mills, E. L., and J. L. Confer. 1986. Computer processing of zooplankton — application in fisheries studies. Fisheries 11: 24–27.

Murtaugh, P. A. 1985. Vertical distributions of zooplankton and population dynamics of *Daphnia* in a meromictic lake. Hydrobiologia 123: 47–57.

Ontario Ministry of the Environment. 1981. Outline of analytical methods. Ontario Ministry of the Environment, Laboratory Services Branch. 246 p.

Persson, G. and G. Ekbohm. 1980. Estimation of dry weight in zooplankton populations: methods applied to crustacean populations from lakes in the Kuokkel Area, northern Sweden. Arch. Hydrobiol. 89: 225–246.

Peters, R. H. 1983. Ecological implications of body size. Cambridge University Press, New York, NY. 400 p.

Roff, J. C., and R. E. Kwiatkowski. 1977. Zooplankton and zoobenthos communities of selected northern Ontario lakes of different acidities. Can. J. Zool. 55: 899–911.

Rosen, R. A. 1981. Length – dry weight relationships of some freshwater zooplankton. J. Freshwater Ecol. 1: 225–229.

Sládaček, V. 1950. Studies of the zooplankton of the ponds of Padrt' (Bohemia) with special reference to the cladoceran *Holopedium gibberum*. Bull. Int. Acad. Cesk. Sci. 51: 175–202.

Sprules, W. G., L. B. Holtby, and G. Griggs. 1981. A microcomputer based measuring device for biological research. Can. J. Zool. 59: 1611–1614.

Stenson, J. A. E. 1973. On predation and *Holopedium gibberum* (Zaddach) distribution. Limnol. Oceanogr. 18: 1005–1010.

Tessier, A. J. 1984. Periodicity of egg laying and egg age distributions in planktonic Cladocera. Can. J. Fish. Aquat. Sci. 41: 409–413.

1986. Life history and body size evolution in *Holopedium gibberum* Zaddach (Crustacea, Cladocera). Freshwater Biol. 16: 279–286.

Tessier, A. J., and C. E. Goulden. 1982. Estimating food limitation in cladoceran populations. Limnol. Oceanogr. 27: 707–717.

Sedimentation Rates and Sediment Core Profiles of ^{238}U and ^{232}Th Decay Chain Radionuclides in a Lake Affected by Uranium Mining and Milling

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Radionuclide concentration profiles in sediment cores from three deep basins of Quirke Lake, Ontario, showed enrichment in the surficial layers related to the period of uranium mining in the watershed, based on sedimentation rates determined from a milling-related pH decline indicated by fossil diatoms. Recent sedimentation rates are 96 ± 7 to 185 ± 14 $g \cdot m^{-2} \cdot yr^{-1}$. ^{210}Pb profiles could not be used to determine sedimentation rates due to loadings of ^{226}Ra and ^{210}Pb from mining and milling activities. Profiles of ^{238}U and ^{232}Th decay chain radionuclides showed an enrichment of 1–3 orders of magnitude in surficial sediments relative to background in deeper sediments. Radionuclide levels in surficial sediments exceeded those reported in lake sediments in uncontaminated systems and, for some radionuclides, approached or equalled levels in sediments contaminated with uranium and radium refining residues. Radionuclide activity ratios in the surficial layers of the Quirke Lake cores and in downstream sediments demonstrated the relative mobilities of the elements in the watershed. Net sediment loading rates for radionuclides in the three basins were 130–230 $mg \cdot m^{-2} \cdot yr^{-1}$ for U, 340–4000 $Bq \cdot m^{-2} \cdot yr^{-1}$ for other members of the ^{238}U decay chain, and 210–530 $Bq \cdot m^{-2} \cdot yr^{-1}$ for ^{232}Th and ^{228}Th.

Des profils de concentrations de radionucléides obtenus de carottes de sédiments prélevées dans trois bassins profonds du lac Quirke (Ontario) montrent un enrichissement des couches superficielles lié à l'exploitation de l'uranium dans le bassin hydrographique. Ce fait est basé sur les taux de sédimentation déterminés à partir d'une baisse du pH liée au broyage et révélé par les diatomées fossiles. Les taux de sédimentation récents varient de 96 ± 7 à 185 ± 14 $g \cdot m^{-2} \cdot a^{-1}$. Les profils du Pb^{210} n'ont pu être utilisés pour déterminer les taux de sédimentation à cause des charges de Ra^{226} et de Pb^{210} provenant de l'exploitation minière et du broyage. Les profils des radionucléides U^{238} et Th^{232} dans la chaîne de désintégration montrent un enrichissement allant de 1 à 3 ordres de grandeur dans les sédiments superficiels par rapport à la concentration ambiante dans les sédiments plus profonds. Les teneurs en radionucléides des sédiments superficiels étaient supérieures à celles des sédiments lacustres de systèmes non contaminés et, pour certains radionucléides, légèrement inférieures ou égales aux niveaux signalés dans les sédiments contaminés par des résidus du raffinage de l'uranium et du radium. Les taux d'activité des radionucléides dans les couches superficielles des carottes du lac Quirke et les sédiments d'aval montrent les mobilités relatives des éléments dans le bassin hydrographique. Les taux de charge nets en sédiments de radionucléides dans les trois bassins variaient de 130 à 230 $mg \cdot m^{-2} \cdot a^{-1}$ dans le cas de l'U, de 340 à 4 000 $Bq \cdot m^{-2} \cdot a^{-1}$ pour les autres membres de la chaîne de désintégration du U^{238} et de 210 à 530 $Bq \cdot m^{-2} \cdot a^{-1}$ dans le cas du Th^{232} et du Th^{228}.

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The uranium mining and milling industry is active in two regions of Canada — near Lake Athabaska, Saskatchewan, and near Elliot Lake, Ontario. These operations release natural radionuclides of the ^{238}U and ^{232}Th decay chains to aquatic and atmospheric environments, primarily from tailings disposal areas. Large amounts of acid, stable trace metals, and milling reagents are also released to the environment by these operations. Once released, radionuclides are transported through environmental pathways and may impact radiologically on human receptors and natural biota.

In freshwater systems, transport of radionuclides is influenced to some degree by sorption onto particulate phases, precipitation reactions, and uptake by biota. Settling of these particulate forms results in a loading to the sediments. As well,

soluble forms of radionuclides may diffuse between lake water and bottom sediments. Sedimentation of radionuclides acts to reduce downstream export and thus moderates the impact of releases in downstream areas. Following the cessation of mining and milling and the reduction or termination of aqueous releases, these contaminated sediments may act as a source of radionuclides to the water column, resulting in long-term impacts.

^{210}Pb and ^{226}Ra of the ^{238}U decay chain have been widely measured in sediment cores to determine sediment accumulation rates in studies on nutrient cycling, trace element loading, particle reworking, and sediment diagenesis (Robbins and Callender 1975; de March 1978; Kipphut 1978; Robbins 1978; Evans and Rigler 1980a, 1980b; Carignan and Flett 1981; Cornwell 1985). Terrestrial and atmospheric loadings and particulate–solute partitioning of ^{238}U decay chain radionuclides were studied in Lake 239 (Experimental Lakes Area, northwestern Ontario; Brunskill and Wilkinson 1987) and in four lakes in the eastern Keewatin District, Northwest Territories (G. J. Brunskill, Freshwater Institute, Winnipeg, Man., pers. comm.), in investigations of radionuclide budgets in watersheds unaffected by the uranium industry.

This study was undertaken to determine accumulation rates and the degree of contamination by ^{238}U and ^{232}Th decay chain radionuclides in the sediments of Quirke Lake, a large Shield lake draining much of the uranium mining and milling district near Elliot Lake. Sedimentation rates were measured to relate the time scale of sediment contamination with the history of mining and milling in the basin. Sedimentation rates are also of concern in light of recent interest in examining the feasibility of deep lake disposal of uranium mill tailings. The burial of emplaced tailings with "clean" sediment after the cessation of mining and milling would result in a barrier to diffusion that would increasingly inhibit remobilization of radionuclides from the sediments back to the water column over the long term.

Lush et al. (1982) modelled the downstream transport, migration through food chains, and effective dose commitments resulting from releases of radionuclides from a hypothetical tailings mass on the shore of Quirke Lake. This model was developed in part as a decision-making tool for regulatory agencies in the management of radioactive releases to surface waters from uranium mines and mills. Model parameters were assigned values based on a review of the literature, rather than on any specific measurements in Quirke Lake or downstream environments. In their sensitivity analysis, the authors found that model predictions (radiation doses) were sensitive to sedimentation parameters in downstream watersheds. The present study provides data on sedimentation rates and net radionuclide accumulation rates for Quirke Lake that may be used in the calibration of such models. Current research is focussing on sediment – porewater distributions of radionuclides, radionuclide concentrations in water-column paticulates, and on measurement of aqueous inputs and outputs of radionuclides in Quirke Lake. Results of this work will be published in the near future.

Sediment chronologies can be determined from ^{210}Pb profiles only in cases where the supply of ^{210}Pb to the sediment occurs at a constant rate, or if the ^{210}Pb supply is proportional to a varying sedimentation rate (Appleby and Oldfield 1983). These assumptions are almost certainly violated in Quirke Lake because uranium milling increases radionuclide loadings to the lake and these loadings vary in quantity and relative proportions of radionuclides depending upon the intensity of mining and milling activity and the wastewater treatment technologies employed.

To overcome this problem, modern sedimentation rates in Quirke Lake were determined by analysis of fossil diatom and pollen profiles in sediment cores. Diatom communities respond to acid loadings by shifting to a more acidophilous species assemblage (e.g. Battarbee 1984; Charles 1985). The sulphuric acid leaching process and the production of pyritic tailings in uranium milling led to the acidification of Quirke Lake beginning around 1957. More recent neutralization of aqueous discharge has permitted a recovery from pH 4.5–5.5 in the early 1960s to pH 5.5–6.4 observed during this study. Diatoms in the core samples were analyzed and lake pH – core depth relationships determined, using approaches similar to those described by Delorme et al. (1984) and Dickman et al. (1984). In Quirke Lake, the decline in diatom-inferred pH was used as a marker for the onset of acidification in 1957, and the mass of more recent sediment accumulation to estimate modern sedimentation rates. Historic sedimentation rates representative of the century preceding the mid-1950s were estimated by analysis of the *Ambrosia* pollen rise in sediment cores (e.g. Huhn 1974; Kemp and Harper 1976; Kemp et al. 1978; Warwick 1980; McAndrews and Boyko-Diakonow 1987).

Study Area

Quirke Lake is a relatively large, deep waterbody (Fig. 1) in the headwaters of the Serpent River watershed draining into the North Channel of Lake Huron. The lake is situated on the Precambrian Shield, approximately 120 km west of Sudbury, Ontario, at 46°30′N, 42°35′W. It is the largest lake in the Serpent River system, with a surface area of 2040 ha, mean and maximum depths of 39 and 102 m, respectively, and a hydraulic detention time of ~5 yr (Snodgrass et al. 1983).

At water depths >3 m, sediments in the lake consist of a dark, fine-grained gyttja with a surficial orange–brown flocculent deposit over about 50% of the lake bottom. Sediments in the deep basins (≥98 m) are brown–black muds, overlain by ~10 cm of an orange–brown layer in the two western basins and by ~10 cm of a light brown deposit in the eastern basin (Fig. 1). We found the orange–brown layer to be rich in iron (unpubl. data). Releases of iron from the mining and milling of pyritic ores are the probable source, although postdepositional diffusion of iron upward in reducing porewaters and precipitation at the oxidizing interface in the surficial sediments (e.g. Carignan and Flett 1981; Cornwell 1985) may contribute to this phenomenon.

The first uranium mine in the watershed began production in 1955. By 1957, there were 11 operating mines in the system. Uranium production decreased in the early 1960s and increased in the late 1960s in response to market demand. There are presently several active and inactive mining and milling operations and tailings disposal sites located within the Quirke watershed. Mill process waters are acidic due to the sulphuric acid leaching process used to dissolve uranium from the ore during milling. This acidity favours the release of radionuclides from the ores. Uranium is removed from the acidic solution, and other dissolved constituents are precipitated by neutralization and discharged with the tailings to the tailings management area. Acidic conditions develop in the tailings due to pyrite oxidation, resulting in the dissolution of radionuclides and subsequent release to surface waters. Acidic conditions

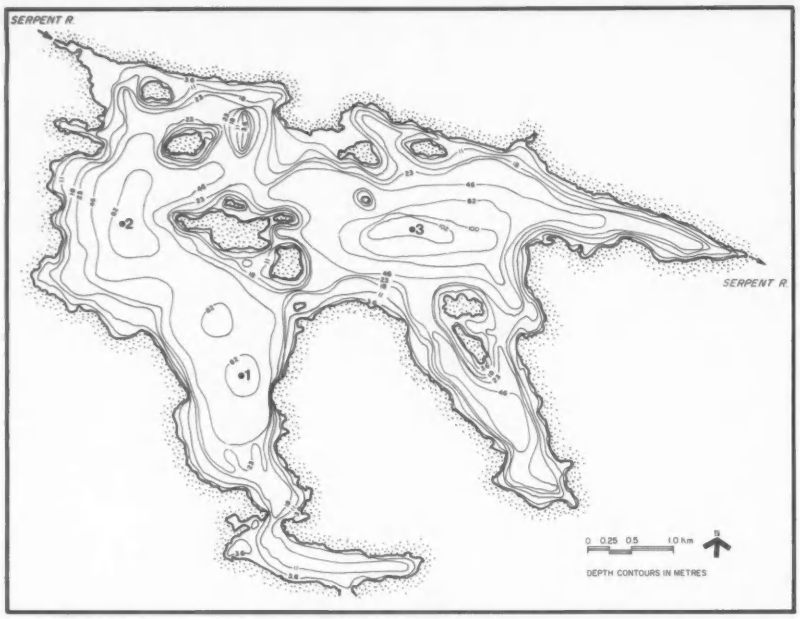

FIG. 1. Bathymetric map of Quirke Lake showing three sediment core sampling stations.

(pH 4.5–5.7) consequently occurred in Quirke Lake in the 1960s and 1970s, with a gradual increase in pH to 5.5–6.4 observed in 1984 (Ontario Ministry of the Environment, unpubl. data) apparently due to improvements in effluent treatment, neutralization of tailings seepage, and improved containment of leachates in new tailings structures over the last 10–15 yr.

Methods

Sediment cores were collected from Stations 1, 2, and 3 at depths of 98–101 m (Fig. 1) in October 1984 using a weighted KB corer outfitted with 4.7-cm (inside diameter) polycarbonate core tubes. Undisturbed cores about 30 cm long were collected with the aid of a CRT-type depth sounder to monitor core entry. Only cores exhibiting a flocculent layer at the sediment–water interface and a layer of overlying water were retained. Five cores were collected from each station — two cores for radionuclide analysis and one core each for diatom analysis, pollen analysis, and dry bulk density determinations.

Cores were sectioned fresh within 24 h of collection. Cores for pollen analysis were sectioned into 1-cm intervals from top to bottom. Before sectioning, horizontal laminations observed in the pollen cores were counted and measured. Cores for diatom analysis were sectioned into 0.2-cm intervals to a sediment depth of 2 cm, 0.5-cm intervals from 2 to 5 cm, and 1- to 3-cm intervals to a depth of 16 cm. Dry bulk densities were determined on 1.5-cm core sections after oven-drying. Duplicate cores for radionuclide analysis were sectioned into six 0.5-cm sections from the surface down to 3 cm; the duplicate sections from each depth were then combined to provide sufficient mass for analysis. One-centimetre-thick sections were taken from one of each duplicate set of radionuclide cores beginning at 3, 4, 6, 9, 14, and 19 cm. Samples for radiochemical analysis were frozen in plastic bags until analysis.

Samples for pollen analysis were first spiked with a known number of *Lycopodium clavatum* spores to permit accurate pollen density estimates (Stockmarr 1970). Fossil pollen was then concentrated from sediment samples with HCl, KOH, and acetolysis solution. Pollen grains and spores were counted until approximately 200 tree and shrub pollen grains per sample were obtained. Pollen was identified following McAndrews et al. (1973). Chronologically significant pollen horizons were expected to occur in more recent sediments; thus, every core section from the surface to 11–15 cm of depth was examined. Only three intervals between 11–15 cm and the bottom of each core were analyzed. Once analyzed, percentage abundance of pollen was used to define pollen zones in the cores based on the rise in weed pollen (*Ambrosia*, Gramineae, Chenopodiineae, *Rumex*, *Plantago*) that can be related to the beginning of farming by European settlers in southern Ontario at about 1830–40 (McAndrews and Boyko-Diakonow 1987).

Core sections for diatom analysis were freeze-dried and blended and 0.05 g was then digested with a mixture of HNO_3 and H_2SO_4. Following washings with distilled water to remove acidity, diatom samples were quantitatively settled onto cover glasses in Battarbee chambers (Battarbee 1973) and then mounted on glass slides using Napthrax, a synthetic resin of high refractive index. At least 500 diatoms per sample were counted.

Several techniques have been developed to assess trends in acidification based on sedimentary diatoms using equations for inferring lake water pH. Problems and uncertainties associated with this methodology are discussed in Davis and Anderson (1984) and Charles (1985). In this study, we assigned each diatom species into one of five categories defined by Hustedt (1939): acidobiontic, acidophilic, indifferent, alkaliphilic, and alkalibiontic. Assignment of diatoms to these categories was

based on the work of Merilainen (1967) and Taylor (1986). Changes in the percent categories in a sediment core were used to reconstruct trends in lake water pH, following the Renberg and Hellberg (1982) index B approach:

$$B = \frac{\%\ \text{indifferent} + 5\ (\%\ \text{acidophilic}) + 40\ (\%\ \text{acidobiontic})}{\%\ \text{indifferent} + 3.5\ (\%\ \text{alkaliphilic}) + 108\ (\%\ \text{alkalibiontic})}$$

The predicted pH − sediment depth profiles were examined, and the historic pH decline was assumed to correspond to the acidification of Quirke Lake caused by the beginning of uranium milling in 1957 in the watershed.

Prior to analysis of radionuclide concentrations or activities, sediments were dried at 50°C and ground to ensure sample homogeneity. Samples for ^{226}Ra and Th isotope analyses were dissolved by KF-pyrosulphate fusion. Samples for total U, ^{210}Pb, and ^{210}Po analyses were digested in a hot, concentrated mixture of HNO_3, $HClO_4$, and HF, followed by a pyrosulphate fusion.

The methods used for radionuclide analysis are detailed in Chiu and Dean (1984) for U, Th isotopes, ^{226}Ra, and ^{210}Pb and in Smithson (1979) for ^{210}Pb. Total U in the solution was determined fluorometrically as its fluoride complex following fusion with NaF−LiF. Th isotopes were determined using high-resolution alpha spectrometry (HRAS). Prior to analysis, ^{234}Th was added to the digested sample as a tracer. Th was coprecipitated with $PbSO_4$, isolated by solvent extraction, and then coprecipitated with cerous hydroxide. The precipitate was beta-counted for ^{234}Th to measure the overall yield and then ^{230}Th, ^{232}Th, and ^{228}Th measured by HRAS. ^{226}Ra was determined by HRAS using ^{133}Ba as a tracer. Ra was coprecipitated with $BaSO_4$ and the chemical yield measured by gamma counting of ^{133}Ba. ^{210}Pb was measured indirectly using ^{210}Bi. The sample solution was held for 30 d prior to analysis to permit greater than 98% ingrowth of ^{210}Bi. A carrier solution of stable Pb and Bi was added before digestion. Bi was then solvent extracted, precipitated as BiOCl, and ^{210}Bi measured by beta-counting. ^{210}Po was measured by HRAS using ^{208}Po as a tracer. Po isotopes were deposited on a nickel disc and the yield measured by recovery of the tracer., Radiochemical determinations were also carried out on one or two UTS reference standards, developed for the National Uranium Tailings Program, Department of Energy, Mines and Resources Canada, for every 15−20 sediment samples analyzed.

Radionuclide counting errors (1σ) were generally ≤12% of total activity for all activity concentrations of ^{210}Pb and ^{210}Po and for ^{226}Ra activities >1 Bq·g^{-1}. Errors were usually ≤25% for Th isotopes at activities of >1 Bq·g^{-1}. At lower activities, counting errors for ^{226}Ra and for Th isotopes generally ranged from 10 to 50%.

Results and Discussion

Sedimentation Rates

Two major pollen zones were found in each core (Fig. 2); Zone 3 is characterized as having <2% weed pollen, while Zone 4 has >4% (pollen zonation as described by McAndrews 1981). Since farming is not widespread in the North Channel region, it is assumed that southern Ontario is the major source of weed pollen in Quirke Lake sediments. Although ragweed (*Ambrosia*) is rare in the Quirke Lake area and northward, it is represented in the pollen record in lake sediments of the region (Huhn 1974). As in southern Ontario, the Zone 3/Zone 4 pollen zone boundary is assumed to be dated at about 1830−40 (McAndrews and Boyko-Diakonow 1987); thus, the overlying sediment represents ~150 yr of accumulation. The 3/4 boundary occurred at sediment depths of 12, 11, and 8 cm in Cores 1, 2, and 3, respectively. Sediments between the 3/4 pollen zone boundary and the diatom-inferred pH decline have accumulated between the beginning of southern Ontario farming and the beginning of uranium mining and milling in the watershed.

The beginning of lake water pH declines, based on diatom-inferred pH, occurred at a sediment depth of 6.5 cm at Station 1 and 4.25 cm at both Stations 2 and 3 (Table 1; Fig. 3). These depths are assumed to correspond to the 1955−59 period. Although the chronology of lake acidification is not precisely known, unpublished records indicate a relatively immediate pH decline following the start-up of uranium mining and milling and acidic conditions (pH 4.5−5.5) in Quirke Lake in the early 1960s. A date of 1957 for the pH decline probably has an uncertainty of ± 2 yr, since mining and stockpiling of pyritic ores began in 1955 and may have caused some acid loading at that time. Large-scale milling (and acid leaching) began in 1957. Based on a lake detention time of 5 yr, an additional 2-yr lag prior to lake acidification is also plausible.

The diatom-inferred pH values derived from the surficial sediment (Fig. 3) are within the present lake water pH range of 5.5−6.4. Furthermore, the inferred pH minima of ~5.4−5.5 for Stations 1 and 2 correspond to reported minima of pH 4.5−5.5 for the early 1960s. However, the inferred pH minimum of 6.0 for Station 3 is at variance with this observation. Inspection of the diatom assemblages from Station 3 reveals a predominance of the pH-indifferent planktonic diatom *Cyclotella stelligera* in deeper sediments, which would tend to overestimate pH. The spatial variability of diatoms in sediments is mainly a function of basin morphometry, and according to the criteria of Earle et al. (1987), planktonic diatoms would tend to be overestimated and littoral diatoms underestimated at Station 3. Station 3 is located in the eastern portion of Quirke Lake and is somewhat isolated from the western portion containing Stations 1 and 2 by a chain of islands. This segregation of the two basins may account for the development of different diatom assemblages in each.

Sedimentation rates calculated from the fossil diatom and pollen data range from 96 ± 7 to 185 ± 14 g·m^{-2}·yr^{-1} (1.6 ± 0.2 to 2.4 ± 0.2 mm·yr^{-1}) for postmining sediments and from 34 to 64 g·m^{-2}·yr^{-1} (0.31 to 0.55 mm·yr^{-1}) for premining sediments (Table 1). Higher recent rates of sedimentation may be related to uranium mining and milling activities. Suspended solids levels may be high in runoff from disturbed areas, and precipitates formed from ferrous minerals dissolved by the milling process may accumulate in Quirke Lake sediments, as suggested by the iron-rich orange−brown deposits observed on the sediment surface. The whole-lake average sedimentation rate in Quirke Lake is probably lower than the accumulation rates found in the three deep basins, due to sed-

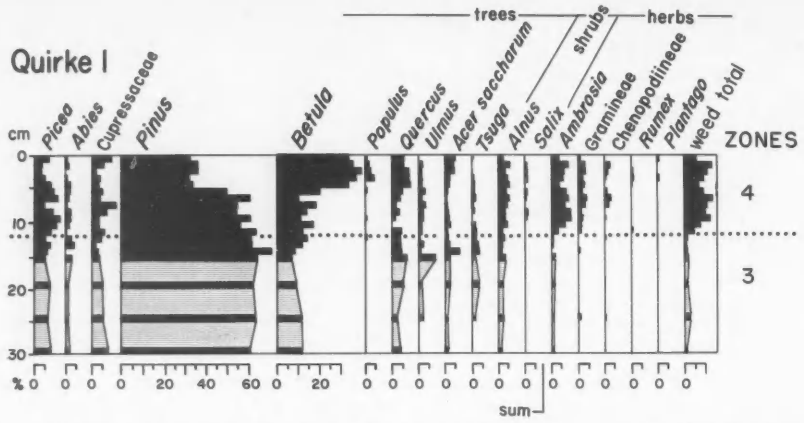

FIG. 2. Pollen diagram from core at Quirke Lake Station 1 showing percentages of main pollen types. Abundance of pollen expressed as percentage of total tree and shrub pollen. Dotted line represents the 3/4 pollen zone boundary (1835).

TABLE 1. Sedimentation rates in Quirke Lake on the basis of fossil pollen and diatoms, Stations 1, 2, and 3. Errors associated with sedimentation rates for postmining zone sediments are based on errors of ±2 yr associated with dating of the acidification of Quirke Lake.

	1		2		3	
Zone	$mm \cdot yr^{-1}$	$g \cdot m^{-2} \cdot yr^{-1}$	$mm \cdot yr^{-1}$	$g \cdot m^{-2} \cdot yr^{-1}$	$mm \cdot yr^{-1}$	$g \cdot m^{-2} \cdot yr^{-1}$
Postmining	2.4±0.2	185±14	1.6±0.2	96±7	1.6±0.2	96±7
Premining	0.45	55	0.55	64	0.31	34

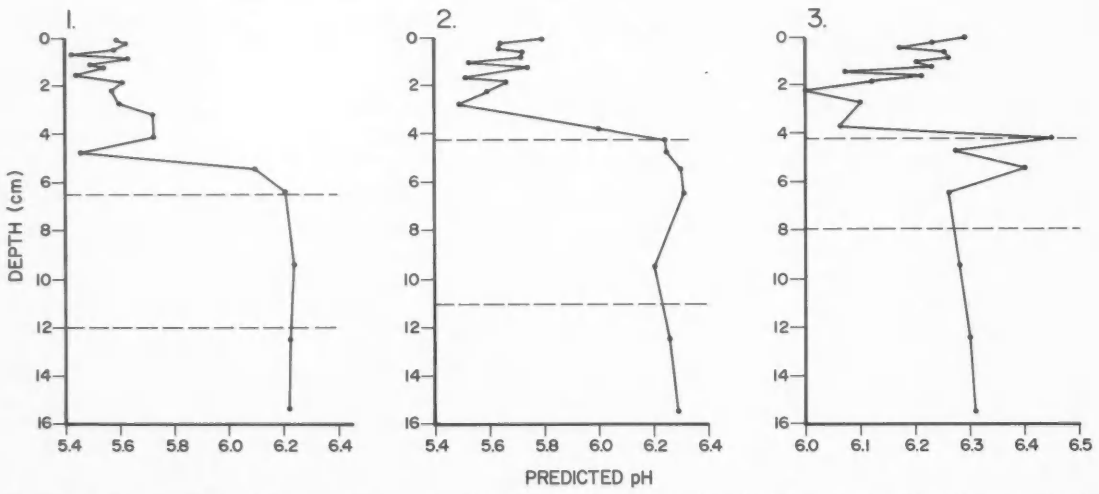

FIG. 3. Sediment core profiles of diatom-inferred pH, based on index B. Broken lines show the 3/4 pollen zone boundaries (lower) and the beginning of the decline in inferred pH (upper).

iment "focussing." Evans and Rigler (1980a, 1983) found that sedimentation rates varied directly with depth in three small Shield lakes in southern Ontario, with depth accounting for as much as 97% of the variation between sites. Accumulation rates were 2–3 times greater in the deep basins than at 10-m depths in these three lakes. Accumulation rates of 96–185 $g \cdot m^{-2} \cdot yr^{-1}$ for recent sediments and 34–64 $g \cdot m^{-2} \cdot yr^{-1}$ for premining sediments are likely close to the maxima for the three basins in Quirke Lake due to suspected relationships with depth. In comparison, Evans and Rigler (1980a, 1983) reported maxima of 226, 133, and 105 $g \cdot m^{-2} \cdot yr^{-1}$ in three southern Ontario Shield lakes. Whole-lake averages for these three lakes were 45–78 $g \cdot m^{-2} \cdot yr^{-1}$. In unproductive Toolik Lake, Alaska, Cornwell (1985) measured sedimentation rates of

12–73 $g \cdot m^{-2} \cdot yr^{-1}$. In unproductive Char Lake in the Canadian arctic, a whole-lake sedimentation rate of 31 $g \cdot m^{-2} \cdot yr^{-1}$ was estimated (de March 1978). G. J. Brunskill (pers. comm.) estimated average sedimentation rates of 22–56 $g \cdot m^{-2} \cdot yr^{-1}$ in four small arctic lakes in the eastern Keewatin District of Canada. These other data suggest that Quirke Lake has exhibited postmining sedimentation rates comparable with those reported for the other Shield lakes and premining sedimentation rates comparable with those found in unproductive arctic lakes. The sedimentation rates reported here in the deep basins of Quirke Lake are representative of potential areas that would be considered for deep lake disposal of tailings. Because tailings disposal would substantially alter the bathymetry of the lake by infilling of the deeper portions of the basin, then these sedimentation rates appear to represent upper limits for the rate of tailings burial following emplacement.

Dark grey to black laminations, separated by lighter reddish grey layers, were observed in the upper 8–12 cm of cores from Stations 1 and 3. No laminations were observed in cores from Station 2. Laminae were variable in thickness, but averaged about 1.4 mm at Station 1 and 0.5 mm at Station 3. If these laminae represent varves, as observed in other Sudbury-area lakes (Huhn 1974), then the inferred sedimentation rates (i.e. 1.4 and 0.5 $mm \cdot yr^{-1}$) are within the range of rates estimated for pre- and post-mining sediments at these stations (Table 1). The presence of these laminations provides evidence that the sediments are relatively undisturbed by processes such as bioturbation.

Core Profiles

Profiles of ^{238}U and ^{232}Th decay chain radionuclides all show enrichment in the surficial 5–7 cm (Fig. 4). The degree of enrichment relative to radionuclide activities in the deep sediments (≥9 cm) is 1–3 orders of magnitude for all radionuclides. Many profiles show diminishing concentrations between the maxima and more surficial sections, apparently demonstrating the effects of recent improvements in wastewater management. The zone of radionuclide enrichment in all cores extends to depths that coincide with or predate the beginning of mining and milling in the Quirke basin. The apparent low level of sediment mixing at Stations 1 and 3, as evidenced by sediment laminations, suggests that the downcore migration of some radionuclides at these stations may be attributed to diffusion. The apparent absence of laminations at Station 2 suggests that sediment mixing may contribute to this downcore migration at this location.

U concentrations of >1000 $\mu g \cdot g^{-1}$ in the surficial core sections of Quirke Lake (Fig. 4) are high relative to sediment U concentrations reported elsewhere. NRCC (1983) reported 1.45–24.7 $\mu g\ U \cdot g^{-1}$ in stream and lake sediments from across Canada. Brunskill and Wilkinson (1987) found 5–6 $\mu g\ U \cdot g^{-1}$ in suspended sediments from Lake 239, and G. J. Brunskill (pers. commun.) found approximately 2–6 $\mu g\ U \cdot g^{-1}$ in bottom sediments from eastern Canadian arctic lakes. In a geochemical survey of 469 lakes in northern Saskatchewan, Coker and Dunn (1983) reported background U concentrations of up to 228 $\mu g \cdot g^{-1}$ in sediments in zones of uranium mineralization, although the geometric mean concentration observed was only 2 $\mu g \cdot g^{-1}$. In Port Hope Harbour, Lake Ontario, U concentrations in surficial sediments also exceed 1000 $\mu g \cdot g^{-1}$ in some locations, due to inputs of residues from uranium and radium refining (Hart et al. 1986). Background concentrations

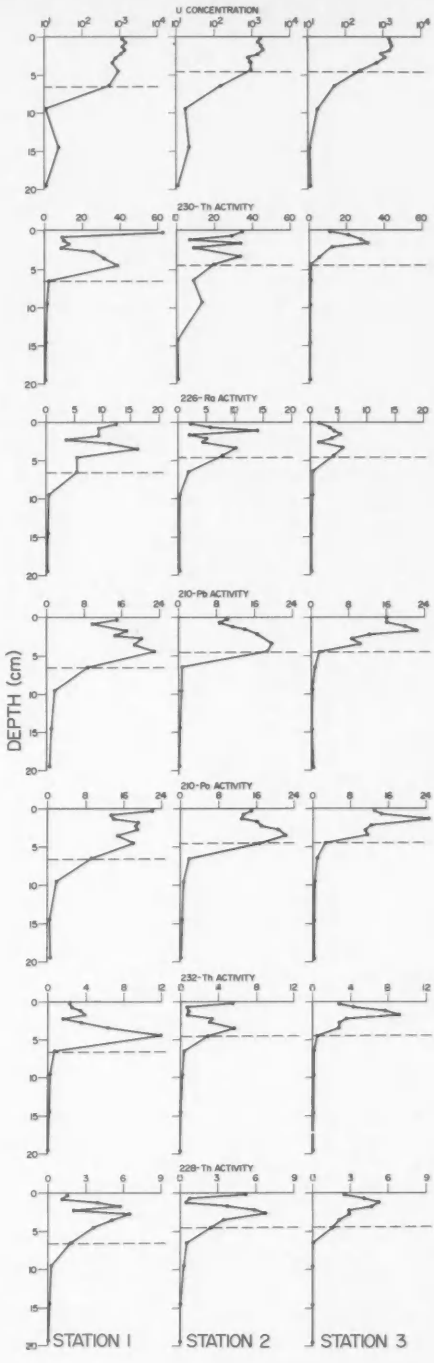

FIG. 4. Sediment core profiles of ^{238}U and ^{232}Th decay chain radionuclides at Stations 1, 2, and 3. U concentrations are in $\mu g \cdot g^{-1}$. Radionuclide activities are in $Bq \cdot g^{-1}$. Broken lines correspond to the beginning of uranium mining and milling (1957), estimated from the diatom-inferred pH decline (Fig. 3).

TABLE 2. Activity ratios in the surficial sediments of Quirke Lake and Serpent Harbour based on mean activities in the surficial 2.5 cm of Quirke Lake cores (this study) and on the mean activities in the surficial 2 cm of sediments from 18 sediment samples collected in Serpent Harbour (Hart and McKee 1985).

	$^{230}Th/^{238}U$	$^{226}Ra/^{230}Th$	$^{210}Pb/^{226}Ra$	$^{228}Th/^{232}Th$
Station 1	1.39	0.41	1.6	1.1
Station 2	1.14	0.26	2.0	1.4
Station 3	1.22	0.17	4.9	0.71
Serpent Harbour	0.33	14	0.76	4.3

of 11–26 μg U·g^{-1} in the deepest two sections of each Quirke Lake core tend toward the high end of the range of U concentrations typically found in lake sediments, apparently reflecting uranium mineralization in the Quirke Lake watershed. The maximum U concentrations in the Quirke Lake cores are equivalent to about 12–15 Bq·g^{-1} on a ^{238}U activity basis. These activities are somewhat less than the maximum activities of ^{230}Th, ^{210}Pb, and ^{210}Po and may reflect not only the greater mobility of U in the aquatic environment, but also the preferential extraction of U in the milling operation. Concentration profiles (Fig. 4) show that the U-enriched layer extends for several centimetres below the 1957 level. This can be attributed to the relatively high mobility of U in the environment (Dyck 1978). Diffusion of uranyl ions downward through the sediment porewater from an oxidizing surficial sediment layer and precipitation as UO_2 in a more reducing, deeper sediment layer may explain this phenomenon.

The activity of ^{230}Th, the first long-lived decay product of ^{234}U, ranges between 10 and 35 Bq·g^{-1} in surficial sediments of Quirke Lake (Fig. 4). While ^{230}Th activities in the surficial sediments of Quirke Lake are high, Hart et al. (1986) reported even higher activities (up to 77 Bq·g^{-1}) in contaminated sediments of Port Hope Harbour. Background ^{230}Th activities of ≤0.05 to 0.5 Bq·g^{-1} in the deepest two sections of each Quirke Lake core are high relative to 0.014–0.016 Bq·g^{-1} in suspended sediment in Lake 239 (Brunskill and Wilkinson 1987) and 0.014–0.048 Bq·g^{-1} in bottom sediment from eastern Canadian arctic lakes (G. J. Brunskill, pers. comm.). Maximum ^{230}Th activities exceed the maximum activities of other ^{238}U decay chain radionuclides (Fig. 4), possibly reflecting the very low mobility of Th in natural waters (Dyck 1978; Langmuir and Herman 1980). Profiles of ^{230}Th show relatively little downcore migration below the 1957 level at Stations 1 and 3, but show substantial enrichment below this level at Station 2 (Fig. 4). This observation may reflect some contamination of the lower profile sediments by the enriched upper layer during the coring process, or may be attributed to sediment mixing at this location, since sediment laminations were not observed at Station 2. Diffusion of Th is unlikely, particularly since there is little evidence for downcore diffusion at the other two stations.

The $^{230}Th/^{238}U$ activity ratios, calculated as means for the top five core intervals, range from 1.14 at Station 2 to 1.39 at Station 1 in Quirke Lake sediments (Table 2). In the surficial sediments of Serpent Harbour, a waterbody at the mouth of the Serpent River watershed, Hart and McKee (1985) observed an average $^{230}Th/^{238}U$ activity ratio of 0.33 for the surficial sediments (Table 2). Th shows a greater affinity for sediment than does U, with a typical particulate–water distribution coefficient of >6500 for Th and 4000 for U in freshwaters (Santschi 1984). Based on the difference in $^{230}Th/^{238}U$ ratios in the upper and lower Serpent watershed and on the greater affinity of Th for the sediment phase, it appears that U is transported downstream much more readily than Th.

The activity of ^{226}Ra, the decay daughter of ^{230}Th, ranges from 2 to 17 Bq·g^{-1} in the surficial enriched sediment of Quirke Lake cores, with activities in most surficial core sections of <10 Bq·g^{-1} (Fig. 3). ^{226}Ra activities of up to 297 Bq·g^{-1} have been observed in the sediments of Port Hope Harbour (Hart et al. 1986). ^{226}Ra activities of 0.032–0.047 Bq·g^{-1} were reported in suspended sediment of Lake 239 (Brunskill and Wilkinson 1987) and 0.008–0.023 Bq·g^{-1} in bottom sediments of eastern Canadian arctic lakes (G. J. Brunskill, pers. comm.); these are below background activities of 0.06–0.28 Bq·g^{-1} found in the deepest sections of the Quirke Lake cores. ^{226}Ra activities in the enriched sections of the Quirke Lake cores tend to be slightly lower than the activities of ^{238}U and ^{230}Th, with $^{226}Ra/^{230}Th$ ratios of 0.17–0.41 for the Quirke Lake cores (Table 2). In contrast, we found ^{226}Ra activities in Serpent Harbour sediments to be about an order of magnitude higher than activities of ^{230}Th (Table 2), indicating that ^{226}Ra is transported downstream more readily than its radioactive parent through the watershed. This is attributed to the lower sediment–water partition coefficient of Ra (typically 200–500; Kirchmann et al. 1966; Nishiwaki et al. 1972; Rancon 1973; Serne et al. 1977) relative to Th.

^{210}Pb, the decay product of ^{226}Ra, occurs in the surficial enriched sediments at activities of 10–23 Bq·g^{-1} (Fig. 4). In comparison, ^{210}Pb activities of up to 682 Bq·g^{-1} were reported in the contaminated surficial sediments of Port Hope Harbour (Hart et al. 1986). The excess of ^{210}Pb relative to ^{226}Ra of up to several Becquerels per gram in the surficial sediments of Quirke Lake results from differences in loading rates of the two radionuclides from mining and milling and the generally greater affinity of Pb for sediments (Snodgrass et al. 1983, 1986; Santschi 1984). The total ^{210}Pb activity from fallout and decay of in situ ^{226}Ra is typically ~0.2–0.4 Bq·g^{-1} in Shield lake sediments (Evans and Rigler 1980a, 1983; Brunskill and Wilkinson 1987); thus, the contribution of fallout ^{210}Pb to substantially greater excesses in Quirke Lake sediments is relatively minor. ^{226}Ra and ^{210}Pb are in approximate equilibrium in the bottom sections of the cores, reflecting decay of excess ^{210}Pb from atmospheric fallout at the time of deposition to activities supported by decay of ^{226}Ra. Mean $^{210}Pb/^{226}Ra$ activity ratios of 1.6–4.9 in the surficial sediments of Quirke Lake and 0.76 in Serpent Harbour (Table 2) further demonstrate that ^{226}Ra is more mobile than ^{210}Pb and is more readily transported downstream.

Within stations, sedimentation rates in pre- and post-mining sediments are within the same order of magnitude (Table 1), while ^{210}Pb activities in each core range over three orders of magnitude (Fig. 4). Thus, the rate of ^{210}Pb supply has changed

markedly over time, and ^{210}Pb profiles cannot be used to estimate sedimentation rates using the "constant rate of supply" or "constant initial concentration" models (Appleby and Oldfield 1983).

^{210}Po, the granddaughter of ^{210}Pb, occurs in the surficial enriched sediment of Quirke Lake cores at activities similar to those of its grandparent (Fig. 4). A slight excess of ^{210}Po relative to ^{210}Pb is suggested in Station 1 and 2 profiles. This can be attributed to analytical error only, since ^{210}Po is supported in the sediment by decay of ^{210}Pb, with secular equilibrium enforced by the short half-life of ^{210}Po. Activities of ^{210}Po in Quirke Lake sediments are substantially lower than the maximum ^{210}Po activity reported in Port Hope Harbour sediments of 739 $Bq \cdot g^{-1}$ (Hart et al. 1986).

Activities of ^{232}Th and ^{228}Th of the ^{232}Th decay chain are 0.5–12 $Bq \cdot g^{-1}$ in the enriched layers of the Quirke Lake cores and ≤0.1 $Bq \cdot g^{-1}$ at the bottom of the cores (Fig. 4), with $^{228}Th/^{232}Th$ ratios ranging from 0.71 to 1.4 (Table 2). These activities are high relative to 0.025 $Bq \cdot g^{-1}$ for ^{232}Th typical of world soils (UNSCEAR 1982), 0.018–0.025 $Bq \cdot g^{-1}$ in suspended sediment from streams flowing into Lake 239 (Brunskill and Wilkinson 1987), 0.044–0.125 $Bq \cdot g^{-1}$ in bottom sediments from eastern Canadian arctic lakes (G. J. Brunskill, pers. comm.), and 0.014–5.2 $Bq \cdot g^{-1}$ in the most contaminated sediments of Port Hope Harbour (Hart et al. 1986). In Serpent Harbour sediments, activities of these radionuclides are 1–2 orders of magnitude lower than in Quirke Lake (Hart and McKee, 1985), suggesting that most of the loading of these radionuclides is sequestered in the sediments in the upper Serpent River system. A $^{228}Th/^{232}Th$ ratio of 4.3 in Serpent Harbour sediments is much greater than corresponding activity ratios of 0.71–1.4 in Quirke Lake (Table 2). ^{228}Ra is a relatively short-lived product (half-life of 6.7 yr) formed in the decay of ^{232}Th to ^{228}Th. A greater $^{228}Th/^{232}Th$ ratio in downstream sediments is apparently the result of more ^{228}Ra being transported than ^{232}Th from tailings areas and through downstream waters. This hypothesis is supported by limited (unpublished) data showing an excess of ^{228}Ra of >2 orders of magnitude relative to ^{232}Th in Quirke Lake water. ^{228}Th forms relatively rapidly (half-life of 1.9 yr) due to ingrowth from this displaced ^{228}Ra and is thereby transported to the sediments at activities exceeding those of ^{232}Th. This phenomenon should also result in $^{228}Th/^{232}Th$ ratios of >1 in Quirke Lake sediments, although the isotopic ratios observed ranged from 0.71 to 1.4 (Table 2) and do not show a definite ^{228}Th excess. The greater mobility of ^{228}Ra has also been reported to result in an excess of ^{228}Th relative to ^{232}Th in oceanic bottom waters (Nozaki et al. 1981).

The net sediment loadings at each of the three Quirke Lake stations may be estimated by multiplying the sediment radionuclide activities in the surficial sections of the cores (Becquerels per gram or micrograms per gram) by the postmining sedimentation rates (grams per square metre per year). These estimates are provided in Table 3 using mean activities or concentrations in the surficial five sections (2.5 cm) of the radionuclide profiles (Fig. 4). ^{210}Po and ^{228}Th are short-lived (half-lives of 138 d and 1.9 yr, respectively) relative to the period of sediment deposition represented by the surficial 2.5 cm. Thus, the activities of these radionuclides in the surficial layer are largely controlled by the activities of their long-lived grandparents, ^{210}Pb and ^{232}Th respectively. Therefore, "accumulation" rates for ^{210}Po and ^{228}Th (Table 3) include the effects of radioactive ingrowth in the sediments. Premining

TABLE 3. Net annual radionuclide accumulation rates for the postmining period (and premining period) at Stations 1, 2, and 3, Quirke Lake, based on estimated mass accumulation rates for postmining sediments (Table 1) and on mean concentrations or activities in the surficial 2.5 cm of sediment cores (Fig. 4). Values in parentheses are based on mass accumulation rates for premining sediments (Table 1) and on mean concentrations or activities in the bottom two core sections (Fig. 4). Units are $mg \cdot m^{-2} \cdot yr^{-1}$ for U and $Bq \cdot m^{-2} \cdot yr^{-1}$ for others.

Radionuclide	Accumulation rate		
	1	2	3
U	230 (1.0)	160 (1.1)	130 (0.4)
^{230}Th	4000 (19)	2200 (25)	2000 (≤2)
^{226}Ra	1600 (11)	570 (9.3)	340 (2)
^{210}Pb	2600	1200	1700
^{210}Po	3200	1400	1600
^{232}Th	500 (5)	210 (2)	530 (≤2)
^{228}Th	540	310	370

period sediment loadings cannot be calculated from radionuclide levels in sediments above the Zone 3/Zone 4 pollen boundary, due to the variable degree of downcore contamination. However, premining loadings may be estimated based on levels of long half-life radionucides in core sections from below the Zone 3/Zone 4 boundary, assuming that sedimentation rates estimated for the 1835–1957 period also apply to these older deposits (Table 3). Estimated postmining sediment loadings in Quirke Lake are about 2 orders of magnitude greater than those estimated for the premining period and >1 to 3 orders of magnitude greater than those found in uncontaminated arctic lakes (G. J. Brunskill, pers. comm.).

The radiological consequences of radionuclide releases to aquatic systems from uranium mining and milling are the focus of concern of regulatory agencies and the general public. Sedimentation is recognized as a mechanism controlling the downsteam transport of radionuclides (e.g. Snodgrass et al. 1983, 1986; Santschi 1984). Estimates of net sediment loadings of radionuclides, as provided herein, are required in the construction of environmental models necessary for the prediction of radionuclide transport and biological impact.

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References

APPLEBY, P. G., AND F. OLDFIELD. 1983. The assessment of Pb-210 data from sites with varying sediment accumulation rates. Hydrobiologia 103: 29–35.

BATTARBEE, R. W. 1973. A new method for the estimation of absolute microfossil numbers, with reference especially to diatoms. Limnol. Oceanogr. 18: 647–653.

1984. Diatom analysis and the acidification of lakes. Philos. Trans. R. Soc. Lond. Ser. B 305: 451–477.

BRUNSKILL, G. J., AND P. WILKINSON. 1987. Annual supply of ^{238}U, ^{230}Th, ^{226}Ra, ^{210}Pb and ^{210}Po to Lake 239 (Experimental Lakes Area, Ontario) from terrestrial and atmospheric sources. Can. J. Fish. Aquat. Sci. 44. (In press)

CARIGNAN, R., AND R. J. FLETT. 1981. Postdepositional mobility of phosphorus in lake sediments. Limnol. Oceanogr. 26: 361–366.

CHARLES, D. 1985. Relationships between surface sediment diatom assemblages and lakewater characteristics in Adirondack lakes. Ecology 66: 994–1011.

CHIU, N. W., AND J. R. DEAN. 1984. Analytical methods manual, National Uranium Tailings Program. A report by Monenco Consultants Limited for Energy, Mines and Resources Canada. (Available from the National Uranium Tailings Program, Energy, Mines and Resources Canada, 555 Booth St., Ottawa, Ont. K1A 0G1)

COKER, W. B., AND C. E. DUNN. 1983. Lake water and lake sediment geochemistry, NEA/IAEA Athabasca test area, p. 117–125. *In* E. M. Cameron [ed.] Uranium exploration in Athabasca Basin, Saskatchewan, Canada. Geol. Surv. Can. Pap. 82–11.

CORNWELL, J. C. 1985. Sediment accumulation rates in an Alaskan arctic lake using a modified ^{210}Pb technique. Can. J. Fish. Aquat. Sci. 42: 809–814.

DAVIS, R. B., AND D. C. ANDERSON. 1984. Methods of pH calibration of sedimentary diatom remains for reconstructing history of pH in lakes. Hydrobiologia 120: 69–87.

DELORME, L. D., S. R. ESTERBY, AND H. DUTHIE. 1984. Prehistoric pH trends in Kejimkujic Lake, Nova Scotia. Int. Rev. Gesamten Hydrobiol. 69: 41–55.

DE MARCH, L. 1978. Permanent sedimentation of nitrogen, phosphorus, and organic carbon in a high arctic lake. J. Fish. Res. Board Can. 35: 1089–1094.

DICKMAN, M., S. DIXIT, J. FORTESCUE, R. BARLOW, AND J. TERASMAE. 1984. Diatoms as indicators of the rate of lake acidification. Water Air Soil Pollut. 21: 375–386.

DYCK, W. 1978. The mobility and concentration of uranium and its decay products in temperate surficial environments, p. 57–100. *In* M. M. Kimberley [ed.] Uranium deposits, their mineralogy and origin. Mineralogical Association of Canada, Short Course Handbook. Vol. 3. University of Toronto Press, Downsview, Ont.

EARLE, J. C., H. C. DUTHIE, AND W. A. GLOOSCHENKO. 1987. Spatial variability of diatoms on the surface sediment of Precambrian Shield lakes. *In* F. Round [ed.] Proc. Ninth Int. Diatom Symp., Bristol, U.K. (In press)

EVANS, R. D., AND F. J. RIGLER. 1980a. The measurement of whole lake sediment accumulation and phosphorus retention using lead-210 dating. Can. J. Fish. Aquat. Sci. 37: 817–822.

1980b. Calculation of the total anthropogenic lead in the sediments of a rural Ontario lake. Environ. Sci. Technol. 14: 216–218.

1983. A test of lead-210 dating for the measurement of whole lake soft sediment accumulation. Can. J. Fish. Aquat. Sci. 40: 506–515.

HART, D. R., AND P. M. MCKEE. 1985. Study to assess the distribution of radionuclides in the aquatic ecosystem in the vicinity of the Serpent River mouth. A report to Environment Canada by Beak Consultants Limited. (Available from D. R. Hart, Beak Consultants Limited, 6870 Goreway Dr., Mississauga, Ont. L4V 1P1)

HART, D. R., P. M. MCKEE, A. J. BURT, AND M. J. GOFFIN. 1986. A benthic community and sediment quality assessment of Port Hope Harbour, Lake Ontario. J. Great Lakes Res. 12: 206–220.

HUHN, F. J. 1974. Lake sediment records of industrialization in the Sudbury area of Ontario. M.Sc. thesis, University of Toronto, Toronto, Ont. 84 p.

HUSTEDT, F. 1939. Systematische und okologische Unterschungen uber die Diatomeen-Flora von Java, Bali, und Sumatra. Arch. Hydrobiol. Suppl. 16: 274–394.

KEMP, A. L. W., AND N. S. HARPER. 1976. Sedimentation rates and a sediment budget for Lake Ontario. J. Great Lakes Res. 2: 324–340.

KEMP, A. L. W., C. I. DELL, AND N. S. HARPER. 1978. Sedimentation rates and a sediment budget for Lake Superior. J. Great Lakes Res. 4: 276–287.

KIPPHUT, G. K. 1978. An investigation of sedimentary processes in lakes. Ph.D. thesis, Columbia University, New York, NY. 180 p.

KIRCHMANN, R. R., A. BOULENGER, AND A. LAFONTAINE. 1966. Absorption of Ra-226. Proceedings of the 1st International Congress of Radiation Protection, Rome. Part 2. 1045 p.

LANGMUIR, D., AND J. S. HERMAN. 1980. The mobility of thorium in natural waters at low temperatures. Geochim. Cosmochim. Acta 44: 1753–1766.

LUSH, D. L., W. J. SNODGRASS, AND P. M. MCKEE. 1982. Aquatic pathway variables affecting the estimation of dose commitment from uranium mill tailings, p. 483–503. *In* Management of wastes from uranium mining and milling. International Atomic Energy Agency, Vienna, IAEA-SM-262/9.

MCANDREWS, J. H. 1981. Late Quarternary of Ontario: temperature trends from the fossil pollen record, p. 319–333. *In* W. C. Maheney [ed.] Quarternary Paleoclimate. GeoAbstracts, Norwich.

MCANDREWS, J. H., A. A. BERTI, AND G. NORRIS. 1973. Key to the Quarternary pollen and spores of the Great Lakes region. Royal Ontario Museum Miscellaneous Publication. 61 p. (Available from J. H. McAndrews, Royal Ontario Museum, 100 Queen's Park, Toronto, Ont. M5S 2C6)

MCANDREWS, J. H., AND M. BOYKO-DIAKONOW. 1987. Pollen analysis of varved sediment at Crawford Lake, Ontario: evidence of Indian and European farming. *In* Geology of Canada and Greenland. Geological Survey of Canada, Ottawa, Ont. (In press).

MERILAINEN, J. 1967. The diatom flora and the hydrogen ion concentration of the water. Ann. Bot. Fenn. 4: 51–58.

NATIONAL RESEARCH COUNCIL OF CANADA (NRCC). 1983. Radioactivity in the Canadian aquatic environment. Associate Committee on Scientific Criteria for Environmental Quality. NRCC No. 19250, Ottawa, Ont.

NISHIWAKI, Y., Y. HONDA, Y. KIMURA, H. MORISHIMA, T. KOGA, Y. MIYAGUICHI, AND H. KAWAI. 1972. Behaviour and distribution of radioactive substances in coastal and estuarine waters, p. 177–193. *In* Radioactive contamination of the marine environment. International Atomic Energy Agency, Vienna, IAEA-SM-185/11.

NOZAKI, Y., Y. HORIBE, AND H. TSUBOTA. 1981. The water column distribution of thorium isotopes in the western North Pacific. Earth Planet. Sci. Lett. 54: 203–216.

RANCON, D. 1973. The behaviour in underground environments of uranium and thorium discharged by the nuclear industry, p. 333–346. *In* Environmental behaviour of radionuclides released by the nuclear industry. International Atomic Energy Agency, Vienna, IAEA-SM-172/55.

RENBERG, I., AND T. HELLBERG. 1982. The pH history of lakes in southwest Sweden, as calculated from the subfossil diatom flora of the sediments. Ambio 11: 30–33.

ROBBINS, J. A. 1978. Geochemical and geophysical applications of radioactive lead, p. 285–393. *In* J. O. Nriagu [ed.] The biogeochemistry of lead in the environment. Elsevier/North Holland, Amsterdam, The Netherlands.

ROBBINS, J. A., AND E. CALLENDER. 1975. Diagenesis of manganese in Lake Michigan sediments. Am. J. Sci. 275: 512–533.

SANTSCHI, P. H. 1984. Radionuclides as tracers for sedimentation and remobilization processes in the ocean and in lakes, p. 338–351. *In* Interactions between Sediments and Water, Proceedings of the 3rd International Symposium, Geneva, August 1984 (extended abstracts).

SERNE, R. J., D. DAI, M. J. MASON, AND M. A. MALICHE. 1977. Batch measurements of nuclides to estimate migration potential at the proposed waste isolation plant in New Mexico. Battelle Pacific Northwest Laboratories Rep. 2448. (Available from Battelle Pacific Northwest Laboratories, Richland, WA 99352).

SMITHSON, G. G. 1979. Radiochemical procedures for determination of selected members of the uranium and thorium series. CANMET Rep. 78–22. (Available from Energy, Mines and Resources Canada, 555 Booth St., Ottawa, Ont. K1A 0G1)

SNODGRASS, W. J., D. L. LUSH, P. M. MCKEE, AND R. R. WALKER. 1983. An approach to the calculation of dose commitment arising from different methods for the long-term management of uranium mill tailings through aquatic pathways. Atomic Energy Control Board Report, INFO-0097. (Available from the Atomic Energy Control Board, P.O. Box 1046, Ottawa, Ont. K1P 5S9)

SNODGRASS, W. J., D. L. LUSH, R. R. WALKER, AND W. BELL. 1986. Particle-based lake model for calculating dose commitment, p. 229–241. *In* P. G. Sly [ed.] Sediment–water interactions. Springer-Verlag, New York, NY.

STOCKMARR, J. 1970. Tablets with spores used in absolute pollen analysis. Pollen Spores 13: 615–621.

TAYLOR, M. C. 1986. Surficial sedimentary diatoms — limnological relationships in Canadian Shield lakes. M.Sc. thesis, University of Waterloo, Waterloo, Ont. 199 p., 42 plates.

UNITED NATIONS SCIENTIFIC COMMITTEE ON THE EFFECTS OF ATOMIC RADIATION (UNSCEAR). 1982. Ionizing radiation: sources and biological effects. Report to the General Assembly, with annexes. United Nations, New York, NY. 773 p.

WARWICK, W. F. 1980. Palaeolimnology of the Bay of Quinte, Lake Ontario: 2800 years of cultural influence. Can. Bull. Fish. Aquat. Sci. 206: 117 p.

Relationship between Bioenergetics and Behavior in Anadromous Fish Migrations[1]

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Minimizing energetic cost per unit distance is often considered the major criterion that anadromous migrants seek to optimize during upstream migration. To test this theory, we documented energetic expenditures and travel speeds of 15 anadromous fish populations involving 9 species observed during their upstream migration. Parameters that characterized fish migratory behavior and the spawning river were calculated for each population. In most cases, cost per unit distance is not minimized and migratory strategy does not conform to the theoretical optimum. Populations that make long or difficult migrations are more efficient in their use of energy reserves than populations that make shorter migrations. Only populations that need all their energy to complete the migration swim at speeds that approach the theoretical optimum. Migration length may lead to improved migratory efficiency by selecting for larger body size, more accurate upstream orientation, and travel speeds that optimize energy efficiency. The failure to minimize energy expenditures is sometimes due to environmental constraints that exceed the physiological capacities of migrants. Minimizing the probablity of death due to exhaustion may be the major factor determining migratory behavior. Selection for energetic efficiency appears important only in cases where energy reserves are exhausted during migration.

Les chercheurs qui étudient le comportement migratoire chez les poissons acceptent de façon générale la minimisation des coûts énergétiques par unité de distance comme facteur d'optimalité régissant les migrations anadromes en rivière. Pour tester cette théorie, nous avons documenté à partir de la littérature les vitesses de déplacement et les dépenses énergétiques qui y sont associées pour 15 populations impliquant 9 espèces anadromes étudiées au cours de leur migration de reproduction. De plus, nous avons calculé une série de paramètres afin de décrire le comportement migratoire des poissons et l'hydrologie du système pour chaque population. Dans la majorité des cas, le coût par unité de distance n'est pas minimisé et la stratégie migratoire observée n'est pas conforme aux prédictions théoriques. Les populations qui effectuent une migration longue et difficile sont énergétiquement plus efficace que celles qui ont une migration courte. Seulement les populations qui utilisent toute leur énergie pour compléter la migration nagent à vitesse proche de la vitesse optimale théorique. Nous proposons que la longueur de la migration peut mener à une efficacité migratoire accrue en sélectionnant les migrateurs démontrant une plus grande taille, une meilleure précision dans l'orientation des mouvements et se déplaçant à vitesse proche de l'optimum. Plusieurs contraintes environnementales peuvent mener à une augmentation des coûts de migration chez certaines populations. La minimisation de la probabilité de mortalité causée par des vitesses de nage élevées pourrait être le facteur principal déterminant le comportement migratoire. Il semble que l'efficacité énergétique soit sélectionée seulement dans les cas où les migrations sont très longues et mènent à l'épuisement des réserves énergétiques.

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The purpose of this paper is to test the hypothesis that anadromous fish behave so as to minimize energy costs per unit distance of migration. We document swimming speeds, travel speeds, and energy costs exhibited by 15 anadromous populations studied from the time of river entry to spawning. In cases where fish do not behave to minimize energy costs per unit distance, we consider the existence of environmental factors that limit the optimal strategy or factors other than energy conservation that determine migratory behavior.

Migration is important in the life cycles of many fish species and is typically considered an adaptation that increases fitness by enhancing growth, fecundity, and survival (Northcote 1978, 1984). It also involves important costs in time, energy, and risk that vary with distance migrated and the difficulties encountered during the trip. The final stages of the reproductive migration of anadromous species involve difficulties like crossing estuaries with tidally induced oscillations in current speed and direction, salinity, and temperature and facing unidirectional currents of up to 5–10 $km \cdot h^{-1}$ near rapids and waterfalls. Anadromous species do not usually feed in freshwater, deriving the energy required for migration from reserves stored in muscles and viscera while at sea. In many cases, gonads ripen during migration, draining even more stored energy. Consequently, reproductive migrations may

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lead to considerable loss of weight and energy which frequently causes high mortalities (Idler and Clemens 1959; Glebe and Leggett 1981b). Thus, one may expect costly migrations to act as strong selective agents for the evolution of traits that improve migratory success. The exceptionally high aerobic metabolic rate and swimming capacity of the sockeye salmon (*Oncorhynchus nerka*) (Brett 1964, 1965a, 1965b, 1967) are good examples of physiological traits appropriate for long and difficult migrations. Chum salmon (*Oncorhynchus keta*) (Beacham 1984) and pink salmon (*Oncorhynchus gorbuscha*) (Beacham 1985) spawning in large rivers have larger heads, fins, and caudal peduncles than do salmon from small rivers, suggesting that water flow velocity leads to morphological adaptations that improve migratory success. River harshness, as measured by the maximum distance that migrants penetrate into freshwater, is known to be correlated with differences in size, age at first reproduction, and date of river entry among populations of Atlantic salmon (*Salmo salar*) (Schaffer and Elson 1975).

One may also expect selection for behavioral traits that adjust time spent migrating and swimming speed to maximize fitness. The use of optimality theory, based on the hypothesis that natural selection tends to produce animals that are maximally efficient at doing all activities associated with propagating their genes (Davies and Krebs 1978), may serve as a general framework for the study of fish migratory behavior. Recently, Pyke (1981) reviewed the more likely optimality criteria for travel speeds and divided them into two main groups according to the purpose of movement. When travel is associated with foraging, animals can regulate their speed to maximize the net rate of energy gain, growth efficiency, or growth efficiency per unit ration (Ware 1975). When travel has nothing to do with foraging (e.g. reproductive migration), speed can be adjusted for minimizing predation (Peterson 1976), minimizing energy expenditure per unit distance (Weihs 1973a; Ware 1978), or minimizing energy expenditure per unit time (Tucker 1968). Any reduction in energy expenditure will permit an animal to accumulate a surplus of energy that may enhance fitness.

Students of fish migratory behavior generally believe that minimizing energetic cost per unit distance is the major criterion in the application of optimality theory to fish migratory behavior. This notion was established by Weihs (1973a) who developed a model, based on the hydrodynamics of swimming, which calculated that fish will minimize the cost of swimming per unit distance if they swim at speeds for which the energy requirement is about twice (1.7–2.3 times) that of the standard metabolic rate. This speed corresponds approximately to one body length per second (1 $Bl \cdot s^{-1}$) but is highly variable depending on species, size, and physiological condition. Subsequently, other models describing the optimal travel strategy in terms of minimizing energy cost per unit distance have been developed (Weihs 1973b, 1973c, 1974; Ware 1978; Pyke 1981; Wakeman and Wohlschlag 1982). However, these models did not consider the importance of water currents, a dominant characteristic of many systems in which fish migrate. Weihs (1978) has shown theoretically that in areas where tides are directional, fish may achieve considerable energy savings by swimming in midwater at a constant speed relative to the bottom when the tide flows in the direction of migration and holding station on the sea floor when the tide flows in other directions. Such behavior, known as selective tidal stream transport, has been demonstrated in plaice (*Pleuronectes platessa*) (Greer Walker et al. 1978) and can save up to 40% in energy cost compared with the alternative strategy of swimming continuously in the direction of overall movement (Weihs 1978). Trump and Leggett (1980) extended the analysis of migratory efficiency by eliminating Weihs's (1978) assumptions of constant current speed and constant swimming speed relative to the bottom. Their model predicts that the optimum swimming speed in a current is $U_0 + 1/b$ where U_0 is the residual or mean current and b is an empirical constant in the expression describing the relationship between swimming speed and oxygen consumption:

$$\log Y = \log C + bu$$

where Y = oxygen consumption (milligrams per kilogram per second), C = standard metabolic rate and u = swimming speed (body lengths per second). The constant b (seconds per body length) varies (according to species) between 0.2 and 0.5; a low value of b indicates an efficient swimmer and a high value indicates an inefficient swimmer (Priede 1985). Trump and Leggett's (1980) model also predicts that energy expenditure is minimized in variable tidal currents by swimming at a constant speed through the water even in cases where occasional retrograde motion over the bottom occurs. This type of behavior has been observed in sockeye salmon migrating in coastal water (Madison et al. 1972) and American shad (*Alosa sapidissima*) migrating in rivers (Leggett 1976).

Few studies of fish migratory behavior test the general hypothesis that anadromous fish behave so as to minimize energy cost per unit distance of migration. Although biotelemetry studies are numerous, the energetic efficiency of swimming behavior often cannot be evaluated because we lack detailed knowledge of speed and direction of the water currents experienced by migrating fish. In addition, biotelemetry studies rarely provide a description of swimming behavior over the total migration route (river's mouth to spawning grounds) because of the short time scales (hours and days) of most tracking studies. However, studies of the energy cost of migration based on observations of weight loss and lipid and protein metabolism, coupled with observations of migration length and duration, provide reliable estimates of energy cost per unit distance for a variety of species and hydrological conditions. When energetic cost per unit time of migration is known, average swimming speeds can be estimated from species-specific respirometry studies relating swimming speed to oxygen consumption. Thus, the combination of these studies can provide estimates of swimming speed (displacement per unit time through the water), travel speed (displacement per unit time over ground), and related energy costs.

Methods and Analysis

Data concerning migration energetics, swimming speed, and hydrology were available for 15 anadromous fish populations involving 9 species (Table 1). Evaluation of the total cost of migration based on the application of caloric equivalents to changes in protein and lipid content of gonads, viscera, and somatic tissues was available for the river lamprey (*Lampetra fluviatilis*) (Moore and Potter 1976), sea lamprey (*Petromyzon marinus*) (Beamish 1979, Beamish et al. 1979), alewife (*Alosa pseudoharengus*) (Parlee 1983), American shad (Glebe and Leggett 1981a, 1981b) Fraser River sockeye salmon (Idler and Clemens 1959), chum salmon (Pentagov et al. 1928),

TABLE 1. Characterisitics of 15 anadromous fish runs obtained from the literature. P
text.

Species (No.)		Migration	Mean weight (g)	Mean length (cm)	km
River lamprey (*Lampetra fluviatilis*)	(1)	Severn	55	30	100
Cisco (*Coregonus artedii*)	(2)	Eastmain	310	29	33
Alewife (*Alosa pseudoharengus*)	(3)	La Have	327	32	32
Sea lamprey (*Petromyzon marinus*)	(4)	St. John (N.B.)	896	77	140
American shad (*A. sapidissima*)	(5)	St. Johns (Florida)	1 000	40	370
American shad	(6)	York	1 300	45	80
American shad	(7)	Connecticut	1 800	55	137
Sockeye salmon (*Oncorhynchus nerka*)	(8)	Skeena	2 200	57	380
Sockeye salmon	(9)	Fraser (Stuart lake run)	2 545	58	1152
Sockeye salmon	(10)	Fraser (Chilko lake run)	2 545	58	596
Atlantic salmon (*Salmo salar*)	(11)	Northwest Miramichi	2 900	74	113
Chum salmon (*O. keta*)	(12)	Amur	3 900	64	1193
Atlantic salmon	(13)	Spey	4 100	77	105
Chinook salmon (*O. tshawytscha*)	(14)	Sacremento	10 000	86	1000
Chinook salmon	(15)	Columbia	15 000	104	1134

[a]Evaluation of the cost of migration does not include the estuary section.

rature. Populations are presented in ascending order of body weight. Data sources are given in the

n th)	Migration length		Relative estuary length	Vertical gradient ($m \cdot km^{-1}$)	Current speed ($BL \cdot s^{-1}$)	Water temperature (°C)	Total migration cost ($kJ \cdot kg^{-1}$)
	km	Body lengths					
	100	3.3×10^5	0.375	0.10	0.60	8	5109
	33	1.1×10^5	0.818	0.45	0.86	11	2114
	32	1.0×10^5	—	—	—	—	884[a]
	140	1.8×10^5	0.321	0.02	—	10	2280
	370	5.9×10^5	0.135	0	—	21	6463
	80	1.86×10^5	0.625	—	—	17	1520
	137	2.49×10^5	0.310	0.22	1.00	16	2863
						13	3778
	380	6.3×10^5	0.131	1.84	3.33		
	1152	1.74×10^6	0.073	0.66	2.32	15	4555
	596	1.0×10^6	—	1.75	2.32	13	5070[a]
	113	1.5×10^5	0.400	1.77	0.54	16	2032
	1193	1.86×10^6	0.084	0.25	1.26	12	6140
	105	1.4×10^5	0.020	—	—	—	1262
	1000	1.15×10^6	0.100	1.00	—	—	3856
	1134	1.10×10^6	0.140	0.53	1.50	15	2852

tion.

chinook salmon (*Oncorhynchus tshawytscha*) (Greene 1926), River Spey Atlantic salmon (Paton 1898), and Eastmain River (James Bay) cisco (*Coregonus artedii*) (Lambert and J. J. Dodson, in prep.). Indirect evaluation of the cost of migration was obtained for Skeena River sockeye salmon (Brett 1983) and was calculated from weight loss measurements during migration for Miramichi River Atlantic salmon (Belding 1934). Changes in tissue mass parallel changes in tissue energy content (Glebe and Leggett 1981b) and thus serve as estimates of energy use during migration. The cost of migration was evaluated as:

$$\mathrm{Mc} = x(a - b) - y(c - d)$$

where Mc = absolute cost of migration (kilojoules), a = net dry weight (total dry weight less gonads) of fish prior to upstream migration (grams), b = net dry weight of fish prior to spawning (grams), c = dry weight of gonads prior to spawning (grams), and d = dry weight of gonads prior to upstream migration (grams). Dry weight was calculated by subtracting moisture content values obtained by Paton (1898) for Atlantic salmon. Protein catabolism accounted for about 20% of the energy liberated during the reproductive migration of River Spey Atlantic salmon (Paton 1898). We assumed a similar situation for Miramichi River Atlantic salmon and calculated that 71% of their dry weight loss was due to lipid depletion and 29% due to protein depletion. Using the energetic equivalents of protein (23.85 $kJ \cdot g^{-1}$) and lipid (38.91 $kJ \cdot g^{-1}$), we calculated an energetic equivalent, x = 34.54 $kJ \cdot g^{-1}$, to convert dry weight to energy loss. A conversion factor, y = 25.52 $kJ \cdot g^{-1}$, was applied to gonad weight, as it represents energy content of gonads of four species (range 24.69–25.94 $kJ \cdot g^{-1}$; Saldama and Venables 1983).

Five environmental variables were used to characterize the freshwater reproductive migration of each population. The first variable considered was the length of the migration measured from the river's mouth to the spawning grounds. Migration length does not include the estuary in the case of the alewife and Chilko sockeye salmon. Migration length in the case of Stuart sockeye is overestimated, as it includes 58 km of coastal migration. Migration length was divided by mean body length in each case to produce an estimate of relative migration length in order to render the values comparable among migrants of different size. The second variable considered was estuary length measured from the river's mouth to the head of the tide. In each case, this value was divided by total migration length to provide an estimate of the proportion of the migration influenced by reversing tidal currents (relative estuary length). Other variables considered were the mean vertical gradient (metres per kilometre) estimated from topographical maps, mean water temperature during the migration, and mean current speed in the river. Mean current speed was divided by mean body length in each case to render current speed data comparable among populations. Current speed data were obtained from the above studies in the case of sockeye and chum salmon populations, from Dodson et al. (1985) for Eastmain River cisco, from Osborne (1961) for Columbia River Chinook salmon, from Stasko et al. (1973) for Miramichi River Atlantic salmon, and from Leggett (1976) for American shad. Water temperature data were obtained from the above studies except in the case of Atlantic salmon (Banks 1969) and American shad (Leggett and Whitney 1972).

Parameter Calculations

The total cost of the reproductive migration for each population was calculated for a female of mean weight for the population. Males were not considered because data were often incomplete. The cost of migration per unit distance (kilojoules per kilometre) or unit time (kilojoules per day) was calculated by dividing total cost by migration length and duration. All estimates are expressed per unit body weight (kilograms) to render the data comparable.

Most published telemetry studies do not provide accurate measures of swimming speed relative to the water because they have not adequately documented current speed and direction experienced by the fish. However, the cost of migration per unit time is a direct consequence of the mean swimming activity of fasting fish. Thus, cost per unit time data permit an estimation of mean swimming speed relative to the water from regressions relating energy expenditure with swimming speed that are empirically determined using respirometry techniques. For example, Brett (1965a) used this method to demonstrate that Fraser River sockeye salmon that expend 177 $kJ \cdot kg^{-1} \cdot d^{-1}$ (Idler and Clemens 1959) were swimming on average at 1.33 $m \cdot s^{-1}$. Mean swimming speed for sockeye, chinook, chum, and Atlantic salmon were predicted using the relationship between energy expenditure per unit time and swimming speed elaborated by Brett and Glass (1973). Results obtained by Bernatchez and Dodson (1985) were used for cisco and American shad and results reported by Beamish (1973) and Claridge and Potter (1975) were used for sea lamprey and river lamprey, respectively.

Mean rate of displacement (kilometres per day) was calculated by dividing migration length by the time from the start of the migration to the spawning period. Observed rates of displacement were noted in some cases, and such values are comparable with our calculated rates. For example, Leggett (1976) observed a mean displacement rate of 6 $km \cdot d^{-1}$ for American shad migrating up the Connecticut River based on telemetry techniques. The mean time from river entry to spawning is 22 d, and the distance covered 137 km for a comparable calculated value of 6.2 $km \cdot d^{-1}$.

Directionality of movement is an important component of migratory behavior. However, quantitative estimates of orientation could not be obtained from telemetry studies, as the typically short observation periods preclude meaningful measurements of directionality, and such studies have not been conducted on all species. Thus, we calculated an index of directionality by dividing the mean rate of displacement by the mean swimming speed relative to the water. The maximum value of the index is 1 and corresponds to an ideal situation where all swimming activity is translated into upstream displacement and, thus, movement is perfectly oriented upstream. Values less than 1 imply either meandering (low directionality, holding position) or the effects of currents; that is, the greater the current velocity the fish must swim against, the greater the swimming activity necessary to cover a unit distance over ground. Although currents surely affect the swimming activity of fish, current speed was not correlated with the directionality index (Spearman's correlation; $r = 0.185$, $p = 0.59$). Thus, we propose that decreasing values of directionality index probably reflect greater meandering behavior and that the index represents a comparative estimate of the directionality and persistence of upstream migration among populations.

To provide a comparative measure of the energetic effi-

TABLE 2. Characteristics of anadromous fish runs calculated from data presented in Table 1.

Species (No.)		Cost per unit distance ($kJ \cdot kg^{-1} \cdot km^{-1}$)	Cost per unit time ($kJ \cdot kg^{-1} \cdot d^{-1}$)	Mean swimming speed ($BL \cdot s^{-1}$)	Mean displacement rate		Directionality index (no units)	Optimal displacement rate ($BL \cdot s^{-1}$)	Optimal displacement index (no units)
					$km \cdot d^{-1}$	$BL \cdot s^{-1}$			
River lamprey	(1)	51.09	34.1	0.33	0.6	0.023	0.070	0.77	0.030
Cisco	(2)	64.06	37.8	0.86	0.6	0.023	0.026	1.16	0.019
Alewife	(3)	27.62	—	—	5.4	0.195	—	0.80	0.244
Sea lamprey	(4)	16.29	27.9	0.13	1.8	0.027	0.207	0.33	0.082
American shad	(5)	17.47	155.1	1.50	8.8	0.254	0.169	0.70	0.363
American shad	(6)	19.00	101.0	1.00	4.6	0.118	0.118	0.65	0.182
American shad	(7)	20.89	130.1	1.09	6.0	0.126	0.116	0.60	0.210
Sockeye salmon	(8)	9.94	179.9	2.77	18.0	0.365	0.132	1.03	0.354
Sockeye salmon	(9)	3.95	168.7	2.71	42.6	0.850	0.314	1.03	0.825
Sockeye salmon	(10)	8.51	117.8	2.25	13.9	0.275	0.122	1.03	0.267
Atlantic salmon	(11)	17.98	16.3	0.10	0.9	0.014	0.140	0.90	0.016
Chum salmon	(12)	5.15	198.1	2.43	45.0	0.814	0.334	1.09	0.747
Atlantic salmon	(13)	12.02	—	—	—	—	—	—	—
Chinook salmon	(14)	3.86	27.6	0.67	7.1	0.096	0.143	1.10	0.087
Chinook salmon	(15)	2.52	66.3	1.40	26.0	0.289	0.207	0.89	0.325

TABLE 3. Spearman correlation matrix. (*$p(r) < 0.05$; **$p(r) < 0.01$; ***$p(r) < 0.001$).

	Cost·distance^{-1}	Weight	Optimal displacement index	Migration length	Directionality	Relative estuary length	Cost·time^{-1}	Current speed	Vertical gradient
Weight	−0.836***								
Optimal displacement index	−0.569*	0.365							
Migration length	−0.779***	0.527*	0.684**						
Directionality	−0.787***	0.576*	0.608*	0.630*					
Relative estuary length	0.736**	−0.615*	−0.811***	−0.577*	−0.722**				
Cost·time^{-1}	−0.209	0.085	0.879***	0.533	0.283	−0.552			
Current speed	−0.644*	0.723**	0.470	0.671*	0.185	−0.571	0.452		
Vertical gradient	−0.350	0.539	−0.021	0.201	−0.088	−0.209	−0.035	0.713*	
Total cost	−0.336	0.045	0.516	0.771***	0.305	−0.352	0.505	0.247	−0.308

ciency of displacement rate, an index of optimal displacement was calculated for each population. The index was calculated by dividing observed displacement rate by a calculated optimal displacement rate. This latter calculation was based on Trump and Leggett's (1980) prediction that optimal displacement rate is independent of current speed and should always equal $1/b$, the theoretical ground speed at which energy cost per unit distance is minimized. Theoretical predictions of this speed were not made in our study. Rather, the empirical least costly ground speed was calculated for each species using the relationships between energy expenditure and swimming speed reported in the respirometry studies cited previously. Our calculated optimal ground speeds (mean of 0.88 $BL \cdot S^{-1}$) fall within the range of Trump and Leggett's theoretical predictions (0.6–2.0 $BL \cdot S^{-1}$). An optimal displacement index value of 1 corresponds to the situation where observed ground speed (displacement rate) minimizes energy cost per unit distance. Index values less than 1 indicate ground speeds that are below optimal, whereas values greater than 1 indicate ground speeds in excess of the optimal displacement rate.

A Spearman correlation matrix was generated to analyse the relationship between the above variables. The null hypothesis that the variables were not correlated was rejected at $p = 0.05$.

Results

Anadromous freshwater migrations are very different in terms of the body size of migrating fish, the type of river, and the distance traversed (Table 1). The total cost of migration is important in each case but varies only by a factor of 5 (1262–6463 $kJ \cdot kg^{-1}$) as compared with the length of the migration which varies by a factor of 36(33–1193 km).

Anadromous migrants do not exhibit a general pattern of migratory performance (Table 2). In some cases, migration can be very slow, involving much meandering and low swimming speed (e.g. river lamprey), or very fast, well oriented and requiring high levels of activity throughout the migration (e.g. Fraser River sockeye salmon and Amur River chum salmon). An important observation is that mean displacement rate never exceeds the optimum displacement rate and is approached only by Stuart Lake sockeye salmon and by chum salmon. Except for these two cases, the rates of displacement represent less than 40% of the optimum.

Increasing energy efficiency of migration is associated with distance traveled, as demonstrated by the strong negative correlation between the cost of migration per unit distance and migration length (Table 3). This relationship is described by an

exponential function (Fig. 1a). Cost per unit distance also decreases exponentially with increasing body weight (Fig. 1b) and as ground speed approaches the optimum (Fig. 1c). Meandering behavior also leads to poor energy efficiency, as illustrated by the strong negative relationship between cost per unit distance and the directionality index (Fig. 1d). Body weight, optimal displacement index, and directionality index are all correlated with migration length (Table 3). In addition, populations that must traverse relatively short estuaries exhibit less overall meandering and travel at speeds closer to the optimum than do fishes that traverse relatively long estuaries (Table 3).

This analysis does not permit us to define the relative contribution of each variable to migratory efficiency because of correlations among variables. The limited number of observations prevents the application of appropriate statistical procedures to quantify the influence of such partially correlated variables. Thus, although the following discussion deals with each statistical relationship as a separate hypothesis, the complex of interrelationships among variables remains to be defined.

Discussion

Energetic Efficiency of Migration

The difference in migratory efficiency among populations is illustrated by the range of energy costs per unit distance (2.52–64.06 $kJ \cdot kg^{-1} \cdot km^{-1}$). The theoretical minimum costs of transport per unit distance, based on Trump and Leggett's (1980) prediction that optimal swimming speeds equals $U_0 + 1/b$ and calculated for those migrations where mean current velocity was available (nine cases, Table 1), vary from 1.10 $kJ^{-1} \cdot km^{-1}$ for Columbia River chinook salmon to 5.88 $kJ \cdot kg^{-1} \cdot km^{-1}$ for river lamprey. Thus, it appears that in cases such as the Stuart Lake stock of sockeye and the chum and chinook salmon analysed, migratory efficiency is close to the theoretical optimum. In most cases, however, cost per unit distance is not minimized and observed migratory efficiency is far from the theoretical optimum.

The observation that energetic efficiency of migration increases with the length of migration (Fig. 1a) is consistent with an evolutionary interpretation of variability in migratory efficiency. Migratory efficiency is a function of the selective pressure imposed by the difficulty of a migration if we assume that the distance to the spawning ground is a major factor contributing to the difficulty of migration (Schaffer and Elson 1975). Our results demonstrate that anadromous populations that make long or difficult migrations are more efficient in their use of energy reserves than populations that make shorter migrations. We propose that the difficulty of migration selects for efficient migrators that are larger, orient more accurately, and travel at speeds that approach the theoretical optimum in terms of energy efficiency.

It has been demonstrated experimentally that larger body size increases metabolic efficiency in terms of energy expended per unit body weight and swimming capacity (reviewed by Beamish 1978). Several authors have provided evidence that the length of migration may have selected for increased body size in Atlantic salmon (Schaffer and Elson 1975) and American shad (Glebe and Leggett 1981b). The results of our survey suggest that previous findings indicating that migration length selects for increased body size and hence greater energetic efficiency may be generalized among anadromous fish populations.

A second factor contributing to migratory cost in the precision and persistence of upstream orientation, with increased meandering leading to increased cost per unit distance. The negative relationship between directionality index and the relative length of the estuary suggests that traversing estuaries contributes significantly to meandering. This phenomenon is illustrated by telemetry studies conducted in estuarine and coastal environments. Much meandering behavior alternating with periods of holding position and retrograde motion is characteristic of American shad (Dodson et al. 1972), Atlantic salmon (Staskso 1975; Brawn 1982), sockeye salmon (Groot et al. 1975), and cisco (Dodson et al. 1985). This behavior is due in part to the physiological stress of passing from saltwater to freshwater. However, such behavior is also associated with problems of orientation. Unidirectional currents encountered above the head of the tide provide strong directional cues and stimulate upstream movement directly by water flowing over the body or by visual, tactile, and olfactory stimuli (Arnold 1974). However, tidally induced oscillations in current direction encountered in estuaries demand tide-specific rheotactic behavior (Dodson and Dohse 1984) or some other mechanism of orientation independent of currents if fish are to avoid swimming back and forth over the same ground. How fish achieve this and the relative precision of the mechanisms of orientation involved remain questions of major interest to students of fish migration (Arnold 1981).

As displacement rate approaches the theoretical optimum, important energy savings can be achieved (Fig. 1c). However, only the Pacific salmon populations surveyed in our study approach this optimal state. Pacific salmon spawn only once in their life and despite their outstanding migratory efficiency, they usually terminate their reproductive migration with metabolic fuel reserves nearly exhausted. Thus, fuel economy is essential for successful reproduction. Iteroparous species such as American shad (Connecticut and York rivers), cisco, Atlantic salmon, and alewife could also benefit from minimizing costs to improve the probability of successfully returning to sea and surviving for future spawnings. This, however, does not appear to be a strong selective factor. Optimal displacement rates that minimize energy expenditure per unit distance are achieved only in cases where migration length leads to extreme energy expenditure.

The Problem of Environmental Constraints

The failure to minimize energy expenditure per unit distance is in many cases due to the presence of environmental constraints that exceed the physiological capacities of migrants. For example, in situations of high current speeds, theoretically optimal ground speeds may be higher than maximum sustainable swimming speeds, resulting in fatigue and long periods of inactivity that permit recuperation. Periods of active swimming followed by periods of holding position during migration in rivers have been documented for several anadromous populations (e.g. Ellis 1966; Leggett 1976; Power and McCleave 1980) although it is not clear whether such behavior is due to fatigue. In some species where swimming capacity has been experimentally evaluated (sockeye salmon, Brett and Glass 1973; cisco, Bernatchez and Dodson 1985), it is clear that current speeds encountered in some parts of the migration must lead to exhaustion.

Some anadromous populations face environmental constraints that force them to spend long periods in rivers without feeding, thus augmenting the cost per unit distance of the

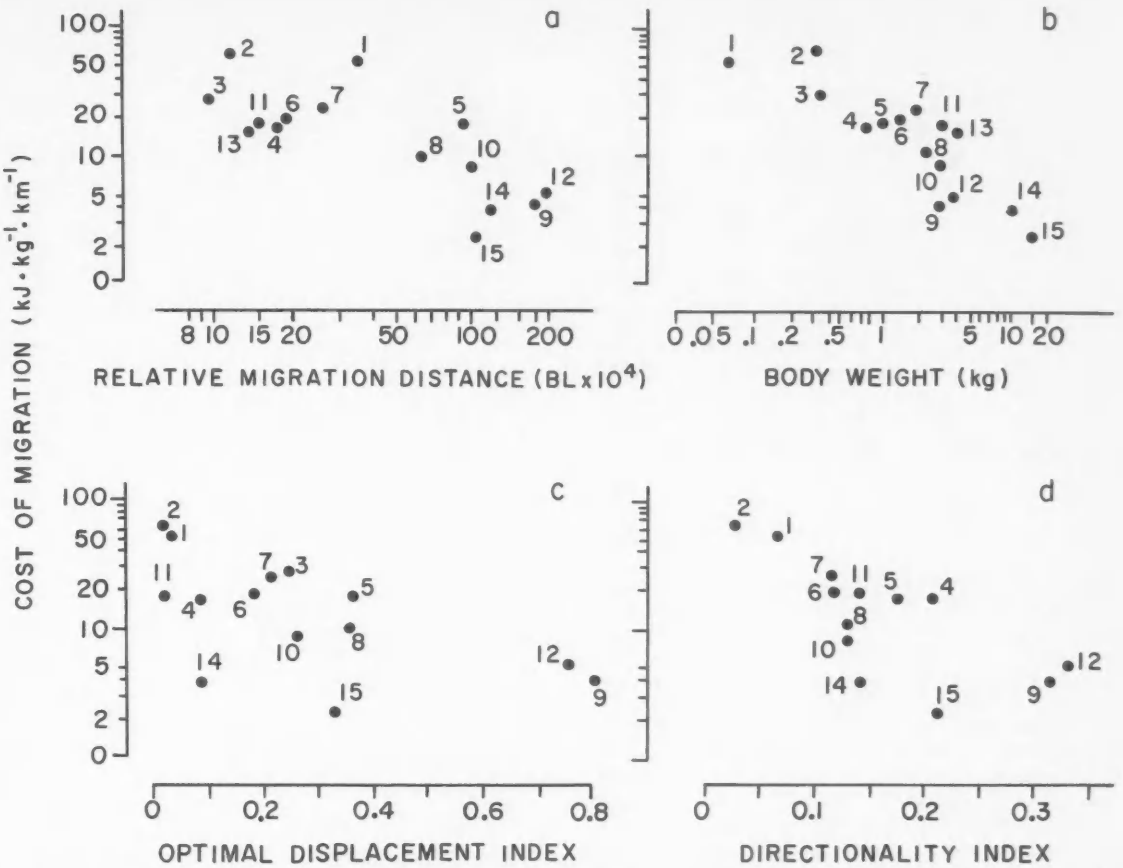

FIG. 1. Relationship between the energetic cost of migration (logarithmic scale) and (a) relative migration distance (logarithmic scale), (b) body weight (logarithmic scale), (c) optimal displacement index (arithmetic scale), and (d) directionality index (arithmetic scale). Numbers refer to anadromous populations identified in Table 1.

freshwater migration. Such situations are particularly evident in northern rivers. Low water temperatures lead to poor swimming capacity by diminishing oxygen uptake and the metabolic scope for activity (e.g. Bernatchez and Dodson 1985) and place a ceiling on the maximum swimming speed attainable by fish (Wardle 1981). We have proposed that such constraints may require cisco to traverse rapids downstream of spawning grounds 6–8 wk before spawning when water temperatures are relatively high (12°C) compared with temperatures at which these fish spawn (<5°C) (Dodson et al. 1985; Bernatchez and Dodson 1985). In the case of Atlantic salmon homing to rivers of Ungava Bay, northern Quebec, Power (1981) hypothesized that sea and river temperatures confine their migrations to a very short period. Adult salmon arrive in the estuaries of their spawning rivers in midsummer as suitable temperatures are attained in Ungava Bay (> 3°C). About 85% of the males have immature gonads when they arrive; they must remain in freshwater over 12 mo before their gonads ripen due to the short period of time during which river temperatures are suitable for maturation. Such protracted periods of freshwater residence, related mainly to temperature constraints, are not unusual among northern anadromous salmonid populations. Arctic char (*Salvelinus alpinus*), studied in the Northwest Territories of Canada, pass 1 yr in freshwater prior to spawning (Dutil 1982).

Power Budgeting vs. Energy Saving

We have until now considered migratory performance only in terms of minimizing energy expenditures per unit distance. However, other biological variables may be more important than energy savings in influencing migratory behavior. A fish working at moderate power outputs may be assumed to have a small probability of mortality, but as metabolic rate approaches the upper limits of metabolic scope, the probability of death due to exhaustion and failure of homeostasis also increases (Priede 1977). Power budgeting refers to the immediate energetic objective of regulating metabolism on a minute-by-minute basis so as to remain within the limits of metabolic scope (Priede 1985). Priede argued that power budgeting may be more important than energy saved in the long-term energy budget. Animals avoid working at high metabolic rates to minimize the probability of mortality; fitness is increased because of increased probability of survival to reproductive age (Priede 1985). Applying this idea to anadromous reproduc-

tive migrations, fish may behave so as to minimize the proportion of time spent at exhausting activity levels to maximize the probability of survival during the migration. However, they must store sufficient energy reserves to afford the increased costs that such behavior may involve. Only in cases of extremely difficult migrations during which all available energy reserves are exhausted does selection for energetic efficiency appear to become important.

The basic assumption that migratory behaviors can be viewed as adaptations for minimizing energy costs is not only inappropriate in many cases but has unduly influenced the way in which we characterize anadromous migrations. Most theoretical treatments emphasize the energetic consequences of different swimming strategies but neglect the precision of upstream orientation. This bias may lead to erroneous interpretations of different swimming strategies. For example, Glebe and Leggett (1981b) predicted that cost per unit distance, based on swimming speed observations, is higher for semelparous than for iteroparous species and concluded that semelparous species swim at speeds close to maximum sustainable whereas iteroparous species swim close to optimum speeds, thereby minimizing the energy costs of migration and improving the probability of return to sea. However, calculations of energy cost per unit distance and optimal displacement index (Table 2) reveal that semelparous sockeye salmon are more energy efficient than iteroparous American shad (Connecticut River stock) in spite of differences in their mean swimming speeds. This difference in overall energetic efficiency can be explained in part by the meandering nature of the shad migration compared with that of sockeye salmon. The fact that precise orientation is not a part of the behavioral repertoire of many migratory fish (Leggett 1984) lends support to the hypothesis that energy efficiency is not the main factor being optimized in most anadromous migrations. The high energetic efficiency and apparently precise upstream orientation of some stocks of Pacific salmon (Table 2) are exceptional and appear to be the result of the selective pressure imposed by the length of migration.

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References

ARNOLD, G. P. 1974. Rheotropism in fishes. Biol. Rev. 49: 515–576.

1981. Movements of fish in relation to water currents, p. 55–79. *In* D. J. Aidley [ed.] Animal migration. Cambridge University Press, Cambridge, U.K.

BANKS, J. W. 1969. A review of the literature on the upstream migration of adult salmonids. J. Fish Biol. 1: 85–136.

BEACHAM, T. D. 1984. Age and morphology of chum salmon in southern British Columbia. Trans. Am. Fish. Soc. 113: 727–736.

1985. Meristic and morphometric variation in pink salmon (*Oncorhynchus gorbuscha*) in southern British Columbia and Puget Sound. Can. J. Zool. 63: 366–372.

BEAMISH, F. W. H. 1973. Oxygen consumption of adult *Petromyzon marinus* in relation to body weight and temperature. J. Fish. Res. Board Can. 30: 1367–1370.

1978. Swimming capacity, p. 101–187. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Vol. 7. Academic Press, New York, NY.

1979. Migration and spawning energetics of the anadromous sea lamprey, *Petromyzon marinus*. Environ. Biol. Fishes 4(1):3–7.

BEAMISH, F. W. H., I. C. POTTER, AND E. J. THOMAS. 1979. Proximate composition of the adult anadromous sea lamprey, *Petromyzon marinus* L., in relation to feeding, migration and reproduction. J. Anim. Ecol. 48: 1–19.

BELDING, D. L. 1934. The cause of the high mortality in the Atlantic salmon after spawning. Trans Am. Fish. Soc. 64: 219–224.

BERNATCHEZ, L. AND J. J. DODSON. 1985. The influence of temperature and current speed on the swimming capacity of lake whitefish (*Coregonus clupeaformis*) and cisco (*C. artedii*). Can. J. Fish. Aquat. Sci. 42: 1522–1529.

BRAWN, V. M. 1982. Behavior of Atlantic salmon (*Salmo salar*) during suspended migration in an estuary, Sheet Harbour, Nova Scotia, observed visually and by ultrasonic tracking. Can. J. Fish Aquat. Sci. 39: 248–256.

BRETT, J. R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. J. Fish. Res. Board Can. 21: 1183–1226.

1965a. The swimming energetics of salmon. Sci. Am. 213: 80–85.

1965b. The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 22: 1491–1501.

1967. Swimming performance of sockeye salmon (*Oncorhynchus nerka*) in relation to fatigue time and temperature. J. Fish. Res. Board Can. 24: 1731–1741.

1983. Life energetics of sockeye salmon, *Oncorhynchus nerka*, p. 29–63. *In* W. P. Aspey and S. I. Lustick [ed.] Behavioral energetics: the cost of survival in vertebrates. Ohio State University Press, Columbus, OH.

BRETT, J. R., AND N. R. GLASS. 1973. Metabolic rates and critical swimming speeds of sockeye salmon, *Oncorhynchus nerka*, in relation to size and temperature. J. Fish. Res. Board Can. 30: 379–387.

CLARIDGE, P. N., AND I. C. POTTER. 1975. Oxygen consumption, ventillatory frequency and heart rate of lampreys (*Lampetra fluviatilis*) during their spawning run. J. Exp. Biol. 63: 192–206.

DAVIES, N. B., AND J. R. KREBS. 1978. Ecology, natural selection and social behavior, p. 1–18, *In* J. R. Krebs and N. B. Davies [ed.] Behavioral ecology: an evolutionary approach. Blackwell Scientific Publishers, Oxford, London, Edinburgh, Melbourne.

DODSON, J. J. AND L. A. DOHSE. 1984. A model of olfactory-mediated conditioning of directional bias in fish migrating in reversing tidal currents based on the homing migration of American shad (*Alosa sapidissima*), p. 263–282. *In* J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill [ed.] Mechanisms of migration in fishes. Plenum Publishing Corporation, New York, NY.

DODSON, J. J., Y. LAMBERT, AND L. BERNATCHEZ. 1985. Comparative migratory behavior and reproductive strategies of the sympatric anadromous coregonine species of James Bay. *In* M. A. Rankin [ed.] Migration: mechanisms and adaptive significance. Contrib. Mar. Sci. 27: 296–315.

DODSON, J. J., W. C. LEGGETT, AND R. A. JONES. 1972. The behavior of adult American shad (*Alosa sapidissima*) during migration from salt to fresh water as observed by ultrasonic tracking techniques. J. Fish. Res. Board Can. 29: 1445–1449.

DUTIL, J. D. 1982. Periodic changes in the condition of the arctic char (*Salvelinus alpinus*) of the Nauyuk lake system. Ph.D. thesis, University of Manitoba, Winnipeg, Man. 149 p.

ELLIS, D. V. 1966. Swimming speeds of sockeye and coho salmon on spawning migration. J. Fish. Res. Board Can. 23: 181–187.

GLEBE, B. D., AND W. C. LEGGETT. 1981a. Temporal, intra-population differences in energy allocation and use by American shad (*Alosa sapidissima*) during the spawning migration. Can. J. Fish. Aquat. Sci. 38: 795–805.

1981b. Latitudinal differences in energy allocation and use during the freshwater migrations of American shad (*Alosa sapidissima*) and their life history consequences. Can. J. Fish. Aquat. Sci. 38: 806–820.

GREENE, C. W. 1926. The physiology of the spawning migration. Physiol. Rev. 6: 201–241.

GREER WALKER, M., F. R. HARDEN JONES, AND G. P. ARNOLD 1978. The movement of plaice (*Pleuronectes platessa*) tracked in the open sea. J. Cons. Cons. Int. Explor. Mer 38: 58–86.

GROOT, C. M. SIMPSON, I. TODD, P. D. MURRAY, AND G. A. BUXTON. 1975. Movements of sockeye salmon (*Oncorhynchus nerka*) in the Skeena River estuary as revealed by ultrasonic tracking. J. Fish. Res. Board Can. 32: 233–242.

IDLER, D. R., AND W. A. CLEMENS. 1959. The energy expenditure of Fraser river sockeye salmon during spawning migration to Chilko and Stuart Lakes. Int. Pac. Salmon Fish. Comm. Prog. Rep. 80 p.

LEGGETT, W. C. 1976. The American shad (*Alosa sapidissima*) with special reference to its migration and population dynamics in the Connecticut River, p. 169–225. *In* D. Merriman and L. M. Thorpe [ed.] The Connecticut River ecological study. The impact of a nuclear power plant. Am. Fish. Soc. Monogr. 1.

1984. Fish migrations in coastal and estuarine environments: a call for new approaches to the study of an old problem, p. 159–178. *In* J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill [ed.] Mechanisms of migration in fishes. Plenum Publishing Corporation, New York, NY.

LEGGETT, W. C., AND R.R. WHITNEY. 1972. Water temperature and the migrations of American shad. U.S. Fish Wildl. Serv. Fish. Bull. 70: 659–670.

MADISON, D. M., R. M. HORRALL, A. B., STASKO AND A. D. HASLER. 1972. Migratory movements of adult sockeye salmon (*Oncorhynchus nerka*) in coastal British Columbia as revealed by ultrasonic tracking. J. Fish. Res. Board Can. 29: 1025–1033.

MOORE, J. W., AND I. C. POTTER. 1976. Aspects of feeding and lipid deposition and utilization in the lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). J. Anim. Ecol. 45: 699–712.

NORTHCOTE, T. G. 1978. Migratory strategies and production in freshwater fishes, p. 326–359, *In* S. D. Gerking [ed.] Ecology of freshwater fish production. Blackwell Scientific Publications, Oxford. 520 p.

1984. Mechanisms of migration in rivers, p. 317–358. *In* J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill [ed.] Mechanisms of migration in fishes. Plenum Publishing Corporation, New York, NY.

OSBORNE, M. F. M. 1961. Hydrodynamic performance of migratory salmon. J. Exp. Biol. 38: 365–390.

PARLEE, T. R. 1983. Lipid and protein content of *Alosa pseudoharengus* (alewife) and *Alosa aestivalis* (blueback) during spawning migrations in the La Have River, Nova Scotia. B.Sc. honours thesis, Dalhousie University, Halifax, N.S. 23 p.

PATON, D. N. 1898. The changes in the fats of muscle, genitalia and other organs of the salmon in fresh water. Investigations of the life history of salmon. Report of the Fishery Board for Scotland. p. 93–139.

PENTAGOV, B. P., YU N. MENTOV, AND E. F. KURNAEV. 1928. Physicochemical characteristics of the breeding migration fast of keta. Bull. Pac. Sci. Fish. Res. Stn. (Vladivostok) 2: Pt. 1.

PETERSON, C. H. 1976. Cruising during migration of the striped mullet (*Mugil cephalus* L.): an evolutionary response to predation? Evolution, 30(2): 393–396.

POWER, G. 1981. Stock characteristics and catches of Atlantic salmon (*Salmo salar*) in Quebec, and Newfoundland and Labrador in relation to environmental variables. Can. J. Fish. Aquat. Sci. 38: 1601–1611.

POWER, J. H., AND J. D. MCCLEAVE. 1980. Riverine movements of hatchery reared Atlantic salmon upon return as adults. Environ. Biol. Fishes 5(1): 3–13.

PRIEDE, I. G. 1977. Natural selection for energetic efficiency and relationship between activity level and mortality. Nature (Lond.) 267: 610–611.

1985. Metabolic scope in fishes, p. 33–64. *In* P. Tytler and P. Calow [ed.] Fish energetics: new perspectives. Croom Helm Ltd., Kent, U.K.

PYKE, G. H. 1981. Optimal travel speeds of animals. Am. Nat. 118(4): 475–487.

SALDAMA, J., AND B. VENABLES. 1983. Energy compartmentalization in a migratory fish, *Prochilodus mariae* of the Ounoco river. Copeia 1983 (3): 617–623.

SCHAFFER, W. M., AND P. E. ELSON. 1975. The adaptive significance of variations in life history among local populations of Atlantic salmon in North America. Ecology 56: 577–590.

STASKO, A. B. 1975. Progress of migrating Atlantic salmon along an estuary, observed by ultrasonic tracking. J. Fish Biol. 7: 329–338.

STASKO, A. B., A. M. SUTTERLIN, S. A. ROMMEL, AND P. F. ELSON. 1973. Migration-orientation of Atlantic salmon (*Salmo salar* L.). Int. Atl. Salmon Symp. Spec. Publ. Ser. 4(1): 119–137.

TRUMP, C. L., AND W. C. LEGGETT. 1980. Optimum swimming speeds in fish: the problem of currents. Can. J. Fish. Aquat. Sci. 37: 1086–1092.

TUCKER, V. A. 1968. Respiratory exchange and evaporative water loss in the flying budgeriar. J. Exp. Biol. 48: 67–87.

WAKEMAN, J. M., AND D. E. WOHLSCHLAG. 1982. Least-cost swimming speeds and transportation costs in some pelagic estuarine fishes. Fish. Res. 1: 117–127.

WARDLE, C. S. 1981. Effects of temperature on the maximum swimming speed of fishes, p. 519–531. *In* M. Ali [ed.] Environmental physiology of fishes. NATO Advanced study Institute Series A, Life Sciences. Vol. 35 Plenum Press, New York, NY. 723 p.

WARE, D. M. 1975. Growth, metabolism and optimal swimming speed of a pelagic fish. J. Fish. Res. Board Can. 32: 33–41.

1978. Bioenergetics of pelagic fish: theoretical change in swimming speed and ration with body size. J. Fish. Res. Board Can. 35: 220–228.

WEIHS, D. 1973a. Optimal fish cruising speed. Nature (Lond.) 245: 48–50.

1973b. Mechanically efficient swimming techniques for fish with negative buoyancy. J. Mar. Res. 31: 194–209.

1973c. Hydromechanics of fish schooling. Nature (Lond.) 241: 290–291.

1974. Energetic advantages of burst swimming of fish. J. Theor. Biol. 48: 215–229.

1978. Tidal stream transport as an efficient method of migration. J. Cons. Cons. Int. Explor. Mer 38(1): 92–99.

Fluctuations of a Fortnightly Abundance Index of the Ivoirian Coastal Pelagic Species and Associated Environmental Conditions

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Mendelssohn, R., and P. Cury. 1987. Fluctuations of a fortnightly abundance index of the Ivoirian coastal pelagic species and associated environmental conditions. Can. J. Fish. Aquat. Sci. 44: 408–421.

In this paper we analyze time series of catch per unit of effort (CPUE) from 1966 to 1982 of small pelagic species off the Ivory Coast using sea surface temperature (SST) collected by merchant ships. A fill-in model is used to estimate missing values of CPUE and SST in the areas in which the fishery operates. A multivariate time series model of the fortnightly data is able to explain 43% of the observed variance in CPUE from 1966 to 1982. A model estimated by using only the data from 1966 to 1980 produced reasonable forecasts of the fortnightly CPUE for 1981–82. A new approach for estimating optimal transformations of variables in the model is used to examine the form of the relationships between CPUE and its predictors. The biological interpretation of the estimated transformations is consistent with previous results on the dynamics of zooplankton in the same area.

Les auteurs analysent une série chronologique de prises par unité d'effort (PUE) de petites espèces pélagiques capturées de 1966 à 1982 au large de la Côte d'Ivoire en fonction des températures de l'eau en surface (TES) relevées par des navires marchands. Ils ont utilisé un modèle à blancs pour déterminer les valeurs manquantes des PUE et des TES pour les pêcheries exploitées. Un modèle des séries chronologiques à plusieurs variables aléatoires pour des données bimensuelles permet d'expliquer 43 % de la variance observée des PUE obtenues de 1966 à 1982. À l'aide d'un modèle généré par les données recueillies de 1966 à 1980, ils ont obtenu des prévisions acceptables des PUE bimensuelles pour 1981–82. Une nouvelle approche pour l'estimation des transformations optimales des variables du modèle est utilisée pour étudier la relation entre les PUE et leurs éléments extrapolés. L'interprétation biologique des transformations estimées est en accord avec les résultats antérieurs sur la dynamique du zooplancton dans la même région.

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The purse-seine fishery for coastal pelagic species off the Ivory Coast annually lands around 20 000 metric tons; this makes the fishery of local socioeconomic importance. The fishery also is of scientific interest because coastal pelagic species are important worldwide and are believed to be significantly influenced by environmental factors (see for example Parrish et al. 1983). The fishery off the Ivory Coast occurs in a region with two upwelling seasons, a smaller one around January and a larger one later in the year, which are followed by periods of strong rainfall, which affects salinity levels in the environment of the fish. Understanding the fishery dynamics in this area and how the dynamics are influenced by the environment can increase our understanding of other pelagic fisheries of greater economic importance.

In this paper our primary goal is to model the relative impact of the environment on the availability of pelagic species off the Ivory Coast in Africa and the manner in which the environment affects the dynamics of catch per unit of effort (CPUE) for these species on time scales as short as 2 wk. Previous studies suggest that the availability and abundance of these stocks are strongly influenced by the environment. Marchal (1967) and FAO (1974) presented evidence that sea surface temperature (SST) and salinity are important influences on the intrayear fluctuations in abundance of these stocks. Annual fluctuations in the abundance indices for the main Ivoirian or Ivoiro–Ghanaian stocks also have been related to changes in upwelling and rainfall (ORSTOM 1976; Binet 1982; Cury and Roy 1985). However, short-term fluctuations of these stocks never have been considered before.

Our approach to this problem is to use multivariate autoregressive moving-average (ARMA) models as described in Tiao and Box (1981) to model and forecast an index of relative abundance for the pelagic species off the Ivory Coast. We also use a new technique developed by Breiman and Friedman (1985) to analyze more closely the form of the relationship between CPUE and the relevant environmental variables. This technique allows us to examine the nonlinearities and discontinuities in the data that a priori are believed to exist but whose

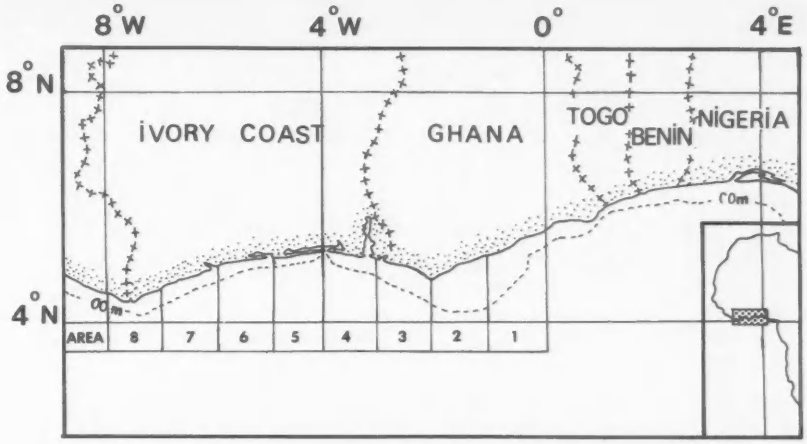


FIG. 1. Location of the areas studied off the Ivory Coast.

exact forms are not known. This should increase our theoretical understanding of how the environment affects the fish stocks as well as have important implications for modeling of fish abundance.

The ARMA class of models are stochastic rather than deterministic and have been of increasing interest in both applied and theoretical aspects of economics and engineering (among other areas). They emphasize the variation in the data and use empirically based methods to determine the proper form of the model. There have only been a few attempted applications of these techniques to fisheries problems (Boudreault et al. 1977; Saila et al. 1980; Mendelssohn 1981).

In contrast with our stochastic models, the majority of fishery management models developed over the last decades have been deterministic models concerned with estimating characteristics of the population at equilibrium (see for example Schaefer 1954; Beverton and Holt 1957; Ricker 1958; Pella and Tomlinson 1969; Fox 1970). Typically, these deterministic models operate on a yearly time scale, and in the best cases provide information related to optimal management of a fishery (such as maximum sustained yield (MSY)) and information necessary to determine policies to achieve this maximum, such as yield per recruit, age of first capture, and other characteristics of the exploited stocks.

Stochastic models of fisheries can be used for forecasting, even if only for short-term forecasts such as a fortnight or a month ahead, and remedy some of the deficiencies of deterministic models. They can be used to improve planning by fishermen and buyers, including both artisanal processors and industrial firms. Many of the exogenous changes that affect a fishery, such as price, or more to the point of this paper, the fluctuations in the physical environment, occur at time scales much shorter than a year. Such stochastic models can improve fishery management by defining the expected level of variation in a fishery and how much of the variation is due to environmental influences.

Biological Data

The fishery exploiting the pelagic species off the Ivory Coast consists mainly of purse seiners that are based in Abidjan. The fishery began in 1955 and expanded rapidly after that. Dependable statistics for the fishery have been available only since 1966 (FAO 1974). The fishery operates mainly over the rather wide continental shelf that exists off the Ivory Coast and Ghana. We have divided the area off the Ivory Coast and Ghana into eight zones, each 1° of longitude and extending from latitude 4°N to the coastline (Fig. 1). Areas 4–7 are the major fishing zones; catch in area 8 is typically less than 1% of the total annual catch, and the areas 1–3 off the coast of Ghana have only been exploited by the Ivoirian purse seiners at irregular intervals. The catch in these areas is dominated by *Sardinella aurita*, which is not the dominant species in the Ivoirian fishery.

During the period 1966–82, *Sardinella maderensis* was the dominant species caught in areas 4–7, comprising 54% of the total catch (Table 1; Fig. 2). *Brachydeuterus auritus* comprised 16.5% of the total catch during the same period, and various other species (Engraulidae, Scombridae, and Carangidae) comprised 14.6% of the catch. All of these species appear to be mainly Ivoirian stocks, as the catch of these species off the coast of Ghana appears to be coming from different stocks (FAO 1974). *Sardinella aurita*, which comprised 12% of the total catch, and *Scomber japonicus*, which comprised 2.4% of the total catch, appear to be shared stocks that are found off the coast of both countries (FAO 1974). *Sardinella aurita* and *S. japonicus* essentially disappeared from the catches in 1973, probably due to a combination of overfishing the previous year and due to anomalous climatic events in 1973. Binet (1982) has discussed this for *S. aurita*. The reasons for the disappearance of *S. japonicus* has not been conclusively determined. *Sardinella aurita* reappeared in 1976 and its relative abundance increased sharply off the Ivory Coast during 1981 and 1982.

The raw data consist of daily records for each boat and for each trip including the areas fished, the areas visited, and the catch. Search time was calculated for each area and fortnight using the method described in Fonteneau and Marchal (1970) and was used as a measure of fishing effort. CPUE was calculated by dividing the total catch of all species in an area during a fortnight by the corresponding search time for that area. When there was no fishing effort the CPUE was assumed to be a missing data point, as the lack of fishing does not necessarily imply the lack of fish. CPUE for the entire area was calculated as the mean of the CPUE of the four zones. CPUE thus is

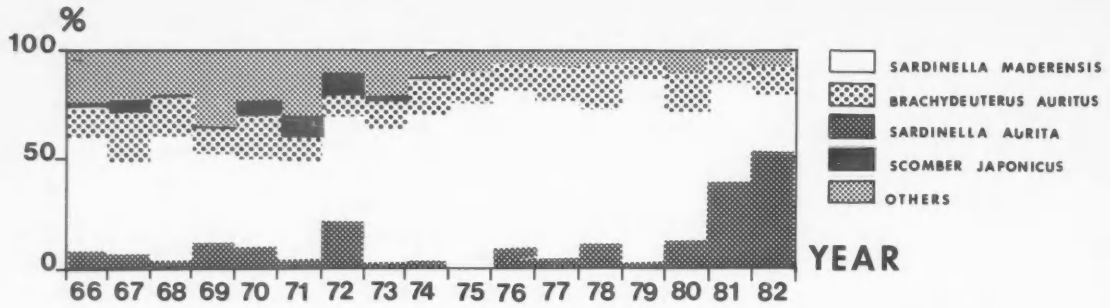


FIG. 2. Specific composition of the total catch of the Ivorian purse seiners in the main fishing areas (zones 4–7).

TABLE 1. Total catch (metric tons) per species for areas 4–7 from 1966 to 1982.

	S. maderensis	*B. auritus*	*S. aurita*	*S. japonicus*	Others	Total
1966	9 305	3662	1 783	262	4697	19 708
1967	8 944	6678	1 886	1405	5389	24 302
1968	12 150	5170	1 165	296	4611	23 391
1969	6 288	2745	2 301	100	5838	17 271
1970	5 794	3477	1 726	1195	3553	15 746
1971	8 629	2718	1 112	2131	5870	20 459
1972	10 742	3000	5 553	2485	2029	23 808
1973	5 368	1275	179	217	1775	8 815
1974	6 823	1850	268	61	1261	10 263
1975	7 805	1639	10	0	956	10 410
1976	10 974	2000	1 457	11	866	15 310
1977	14 898	3413	855	0	1398	20 563
1978	10 325	3568	1 892	6	923	16 716
1979	14 709	1208	439	0	912	17 268
1980	8 196	2572	1 789	0	1616	14 171
1981	9 790	2418	8 747	4	836	21 796
1982	5 108	2463	10 637	0	1608	19 815

defined in units of metric tons per day of fishing.

For CPUE to reflect the abundance of a fish that schools and whose schooling behavior changes rapidly, the measure used should reflect the number of schools present and the size and spatial distributions of both the fleet and the stock. Ignoring fishing, the boats can be viewed as taking a sample during each time period to provide an estimate of the abundance of the fish stock. From sampling theory we know that if there are too few boats out "sampling" (fishing) or if their spatial distribution is not appropriate to the target population, the estimates of abundance will be very inaccurate. Similarly, sampling needs to reflect the relative frequency of different school sizes if abundance estimates are to be accurate.

The measure of effort we use considers total search time, but does not consider either the number of boats searching or school size distribution. Thus, our measure will not always reflect abundance, particularly when there have been only a few boats out searching. More boats searching should also produce a less variable estimate of CPUE due to a more uniform coverage of the fishing area. This may explain the increased variability in the CPUE series after 1973, when the number of boats fishing decreased from 40 to fewer than 20.

Environmental Data

The environmental series considered in preliminary model identification consist of SST data collected by merchant ships passing through the area. The SST data were obtained from the National Climate Center (U.S.), and values were checked against a long-term atlas and further verified by C. Roy of ORSTOM. Fortnightly mean values then were calculated for the SST series by area, to agree with the fishery data, and for the two coastal environmental series.

The continental shelf off the Ivory Coast is influenced by two periods of upwelling. The main upwelling season occurs from June to September and a second, smaller upwelling occurs in January and February (Morliere 1970). The physical mechanisms underlying these upwellings are summarized and discussed in Picaut (1983, 1985). One of the reasons SST was selected as an environmental series is that it should be a reasonable surrogate variable for the occurrence of upwelling in the region.

Preliminary Data Analysis

Preliminary analysis of the data is necessary for two reasons. We consider areas that have no fishing as having missing data points and there are also areas with missing environmental data; most of our techniques, however, require complete data series. Therefore we must fill in the missing data in a manner that will not distort the underlying relationships in the data.

Also, the ARMA approach to model building is empirical, using properties of the covariance structure of the data to determine the appropriate form of the model to be estimated, rather

than hypothesizing a model a prior. The form of the estimated lagged covariance matrices and generalized partial-correlation matrices are used to make initial estimates of the appropriate lags and variables to be included in the model.

The first step in the preliminary analysis is to fill in the missing data by area. Areas 4–7 have roughly 4% of the CPUE data missing. Also, during the years 1969 and 1982 there was a large gap in the SST data in all the areas. The CPUE data were filled in using an algorithm by Shumway and Stoffer (1982), used successfully in a related analysis by Mendelssohn and Roy (1986). The algorithm is described in the Appendix.

The basic idea of the algorithm is to iteratively fit a lagged model to the completed series and then to calculate minimum mean-square estimates of the missing data given the new parameter estimates. The algorithm has good statistical properties (see Shumway and Stoffer 1982), particularly in terms of preserving the covariance structure of the observed series. Other more obvious methods do not share this property. Also, the algorithm includes observation error in calculating both the parameter estimates and the smoothed estimates of the missing data.

The algorithm calculates smoothed values rather than predicted values of the missing data. Predicted values use only information previous (or perhaps contemporaneous) to the missing data point to estimate the fill-in. Smoothed values use all the information available consistent with the model. Thus, for an AR(2) model, the filled in value is calculated from a forward model using data from the last two periods, from a backward data using the next two periods of data, and from a regression-like model using contemporaneous innovation series.

The fill-in model for CPUE uses the observed data from each area and the model form to fill in any missing point. While this may cause some bias in our later analysis, it is a conservative procedure for several reasons. First, as one of our main interests is the role of the environment in the population dynamics, any bias introduced should be to lessen the importance of the environment as a predictor and to increase the importance of lagged values of CPUE as predictors. Also, we use average CPUE (across areas) in our final model. Thus most of the filled in values are averaged with real values from other areas, lessening the impact on the data of any of the filled in values. With only 4% of the data missing, a filled in data point would have to have significant leverage to greatly influence the final model.

The SST data were filled in using both the Shumway and Stoffer algorithm and the estimated seasonal cycle. The iterative algorithm produced data values for the missing blocks in 1969 and 1982 that did not appear reasonable; however, the spectra produced by this procedure were very consistent with those calculated from complete subseries of the SST data. Parameter estimates depend on the covariances of the data, so that the bad data values may not be important. Using the estimated seasonal cycle can produce its own distortions, as the missing year may have been very unlike the normal year. This can greatly emphasize the seasonal frequency in the data while lessening other frequencies that might be of importance in determining the appropriate model.

Fortunately, our results were almost identical for each method of filling in the SST data. Preliminary reviewers of our results felt more comfortable with using the estimated seasonal cycle; therefore, in what follows, the SST data have been completed using the estimated seasonal cycle.

The smoothed values for CPUE by area (Fig. 3) appear to be quite reasonable. None of the estimated values appear as particular outliers, which reinforces our belief that this should produce little bias in our final calculations.

We do not use effort at time t (i.e. no lag) as a predictor because this would introduce a large bias and a high degree of spurious correlation into the analysis. This point is shown mathematically in Eberhardt (1970); Mendelssohn (1981) gives other references that examine the degree of spurious correlation introduced.

An intuitive explanation of the source of this spurious correlation can be seen by considering log (CPUE) which equals log (catch) − log (effort). If this is regressed against a function of effort, then effort is clearly on both sides of the equation. If the coefficient of variation (CV) of catch is small compared with that of effort, then catch can be viewed as a constant, and we would be regressing a function of effort (the logarithm of effort) against another function of effort, so that some degree of fit is assured. Simulations in the references suggest that the r^2 value can be inflated by as much as 0.4–0.6 depending on the relative values of the CV of catch compared with the CV of effort.

The accuracy of the completed time series of CPUE and SST (Fig. 3 and 4) can be assessed in several ways: by comparing smoothed values with observed values when both exist; and by comparing smoothed values with observed values in other series where the data exist to check that the smoothed value is consistent. For the CPUE series, which are relatively complete, the smoothed values can be seen to be very close to the observed values, even at large peaks in CPUE, such as in area 4 during 1976 (Fig. 3a).

The parameter estimates produced by the AR(2) fill-in model for CPUE (Table 2) are of interest by themselves, as they appear to agree with and clarify previous work on migration in the stocks. The interpretation of the model for CPUE will be discussed in detail in a companion paper on the spatiotemporal dynamics of the fish. In what follows, we restrict our attention to CPUE and SST averaged over all of the areas.

Model Identification and Estimation

We model the temporal dynamics of CPUE and its possible relationships with SST by using for the most part the ARMA approach described in Tiao and Box (1981) and implemented in the computer program WMTS-1 (Tiao et al. 1980). At times, a method due to Akaike et al. (1979) for subset multivariate autoregression identification was also used to help select the appropriate lags and the parameters to be included in the model at those lags.

For several reasons, we analyze the natural logarithm of CPUE (actually of CPUE + 0.05 so that zero values are well defined) rather than analysing CPUE itself. First, CPUE is a ratio of two separate series, and ratios rarely are linear or gaussian in distribution. Taking logarithms of the data produces a new series that is the difference of the logarithms of the two original series, which should have better statistical properties. Second, inspection of the raw data (Fig. 4a) suggests that the variance of the series changes with the level of the CPUE series. A range–mean plot (Jenkins 1979, p. 96) of the CPUE data was calculated. This is found by dividing the series into a number of subseries (in this case years), calculating the range and mean of each subseries, and plotting the range versus the mean. This plot showed that a transformation such as a log

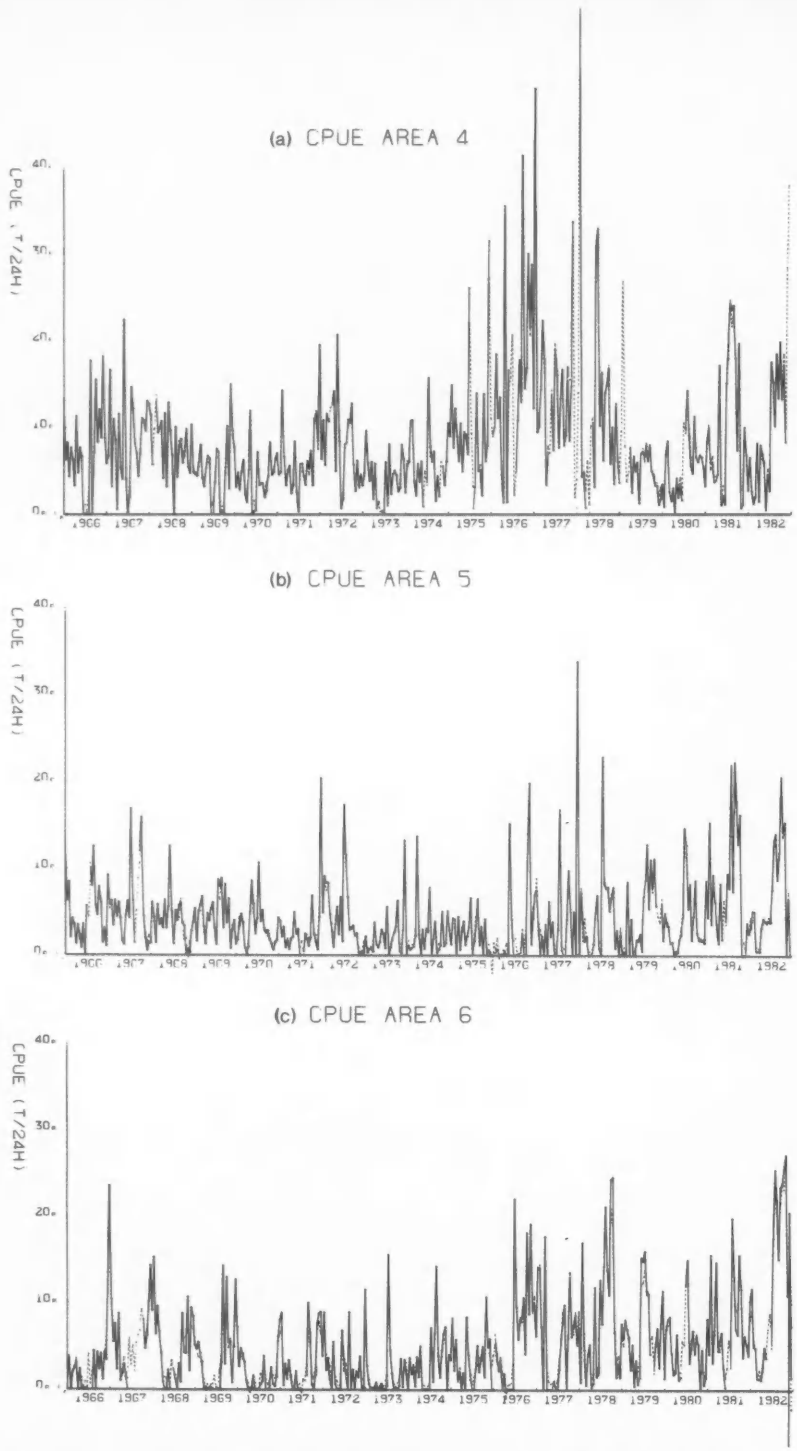


FIG. 3. Time series of CPUE (all species) for (a–d) areas 4–7 and (e) all areas combined. Solid lines = observed; broken lines = smoothed. (*Fig. 3 concluded next page*)

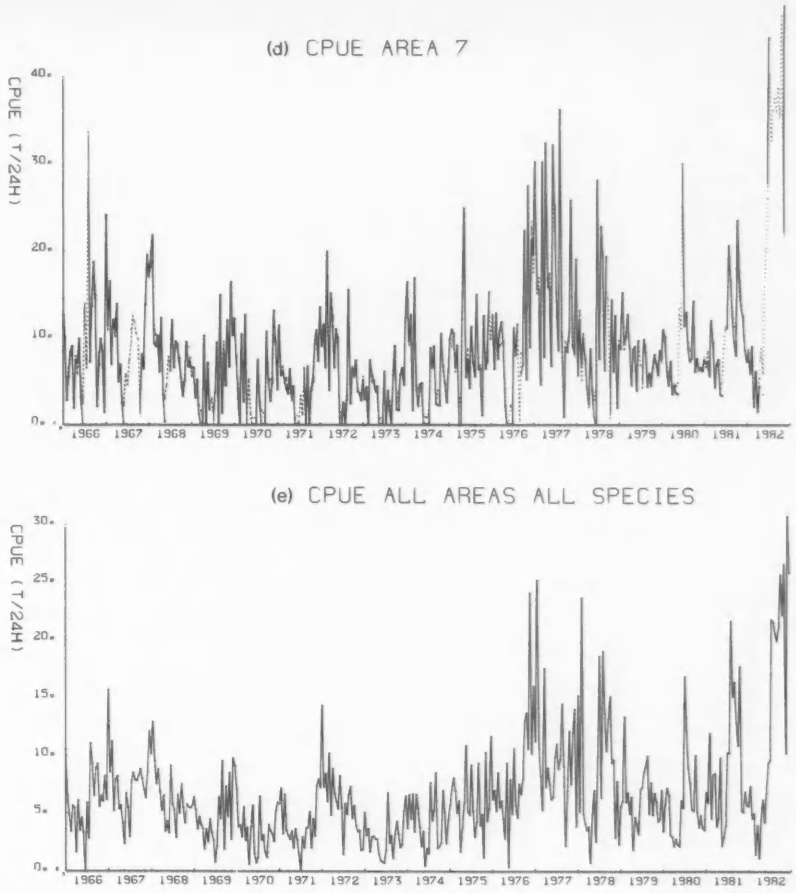


FIG. 3. (*Concluded*)

transform or a negative square root transformation was needed. Third, there are theoretical reasons for believing that a log scale is more appropriate for modeling the interaction of CPUE with SST. On the untransformed scale, a 1° change in SST would have to make the same absolute change in CPUE at very low levels of CPUE as with very high levels of CPUE. When ln (CPUE + 0.05) is used, a 1° change in SST produces a percentage change in the level of CPUE rather than an absolute change. Thus, at much smaller levels of CPUE, smaller absolute changes in the level will be observed. In the next section, we will examine in more detail the proper scales for each of the variables in our model and the form of the interactions between the different variables.

The first step of the analysis is to identify the appropriate lags to be included in the model and whether an AR, MA, or ARMA model is more appropriate. This is done by examining the cross-correlation matrices and by calculating the general partial-correlation matrices (see Tiao and Box 1981 for details). The CPUE autocorrelation function (not shown) has significant lags up to 8 fortnights, and again around 24 fortnights (1 yr), although the pattern is not that of a seasonal cycle in the data. (A seasonal cycle is reflected in a sinusoidal autocorrelation function. The autocorrelation function of SST is sinusoidal, reflecting a seasonal cycle, while CPUE only has a peak at a lag of 24 fortnights. To call this a "cycle" would be equivalent to saying a peak at lag 1 shows a one-fortnight cycle.) The pattern in lags 1−8 suggests significant values at lags 1, 2, and 4 and possibly at lag 6. This is because autoregressive terms decay exponentially. Thus, if there is a significant autocorrelation at lag 1, then lag 2 will have an autocorrelation of that value squared, even if there is no lag 2 effect. Similarly, if there is a lag 2 term, then lag 4 will have that value squared even if there is no lag 4 effect. Thus, we look for the autocorrelations that stand out from the exponential decay of the previous significant lags.

The cross-correlation function (not shown) shows a significant peak and exponential decline with SST lagged 17 fortnights and significant cross-correlations with SST lagged until about 8−10 fortnights. The generalized partial-correlations (Table 3) exhibit "spiked" behavior consistent with an AR-type model at the lags suggested by the cross-correlation matrices.

An exact maximum likelihood algorithm was used to estimate the parameters of this model, which also included parameters modeling the SST series. This last step is important so that the final vector residual series are as close as possible to independent multivariate gaussian variables. Otherwise, the esti-

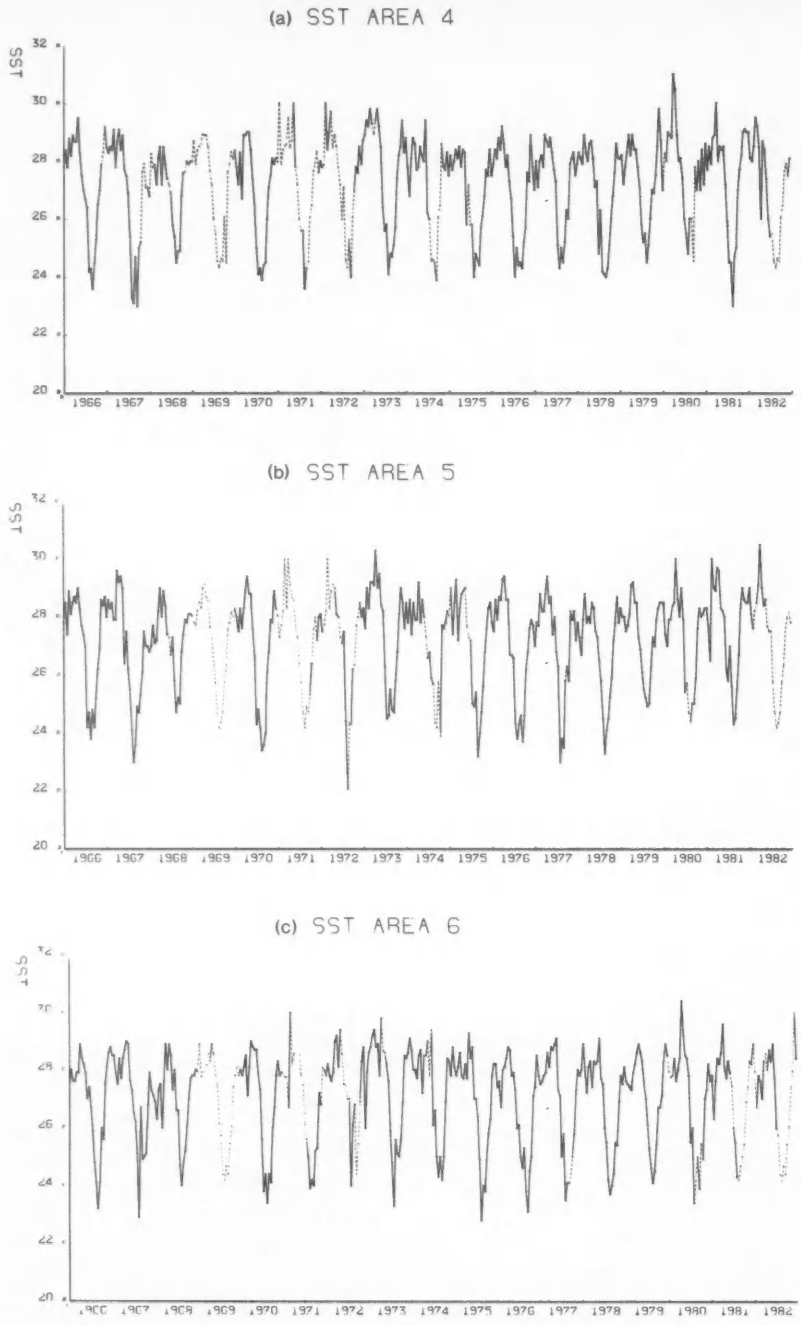
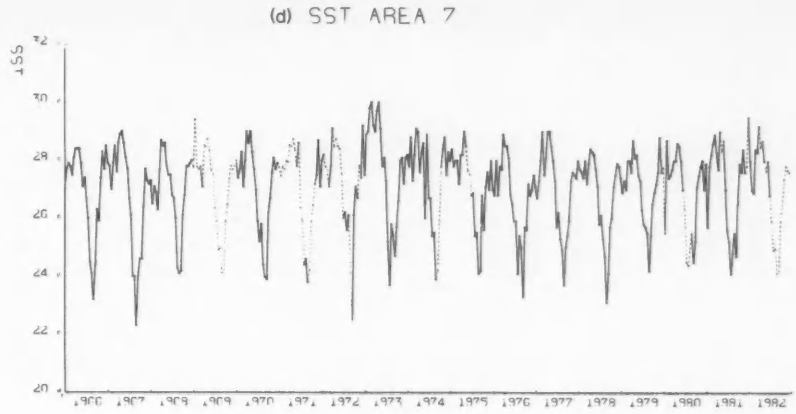


FIG. 4. Time series of SST for (a–d) areas 4–7 and (e) average of all areas. Solid lines = observed; broken lines = smoothed. (*Fig. 4 concluded next page*)

mates can be biased. The relationships between CPUE and SST at lags 6 and 7 were found to be nonsignificant. They were discarded from the model, and the remaining parameters were reestimated.

The final parameter estimates and their standard errors (Table 4a) were tested for adequacy by several methods. The residual cross-correlation matrices do not suggest a lack of fit (Table 5). The residual series (not shown) have a zero mean and otherwise do not suggest a lack of fit to the data. The normalized residuals for CPUE (not shown) are nearly gaus-



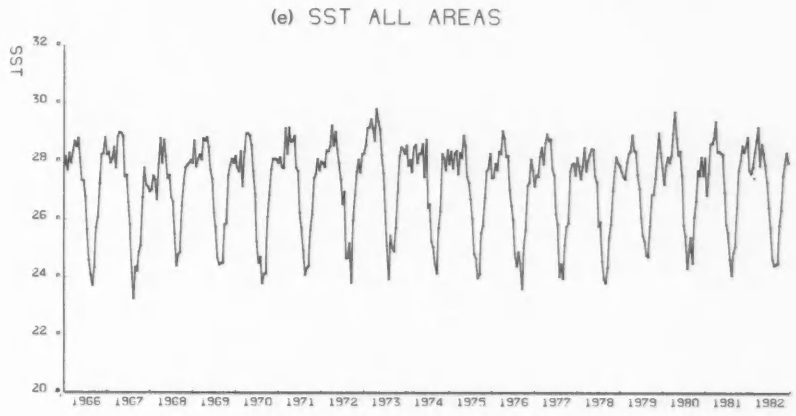


FIG. 4. (*Concluded*)

TABLE 2. Values of coefficients of the fill-in models for CPUE time series ($t-1$, $t-2$) in areas 4–7.

	Area 3		Area 4		Area 5		Area 6		Area 7		Area 8	
	$t-1$	$t-2$	$t-1$	$t-2$	$t-1$	$t-2$	$t-1$	$t-2$	$t-1$	$t-2$	$t-1$	$t-2$
Area 4	0.11	0.02	0.24	0.20	0.20	0.10	−0.51	0.34	0.22	0.06	0.11	−0.05
Area 5	0.01	−0.02	−0.07	0.19	0.40	0.09	0.02	0.07	−0.04	−0.14	−0.01	−0.11
Area 6	0.07	−0.03	0.08	−0.01	0.04	−0.01	−0.38	0.18	−0.02	0.10	0.17	−0.14
Area 7	−0.01	−0.16	0.08	0.09	0.09	−0.05	−0.04	0.44	0.31	0.53	−0.10	−0.13

TABLE 3. Significance (5%) of partial autoregression coefficients by lag for time series of CPUE and SST.

	Lag									
	24	17	1	2	3	4	5	6	7	8
LNCPUE	+		+	+		+				
SST	−	+	−	+				−	−	

sian, with a mean of zero and a median close to zero. The distribution of the normalized residuals is fairly symmetric also. There are two noticeable outliers, each with a normalized value greater than 4. These two points account for almost 10% of the residual variance. Both are from fortnights when there was only one boat searching, and from the data it is quite clear that in each instance the boat was just passing through the area to fish in another area. This is consistent with our previous discussion of problems with the measure of effort used.

The model was also estimated using the fill-ins for SST produced by the Shumway and Stoffer algorithm (Table 4b). There is essentially no difference, giving us some confidence that our model is robust to the method of completing the data series. Both models were reestimated for the years 1966–82. In 1981 and 1982, there was a sharp increase in the level of CPUE, and also a change in the species composition, with an increasing amount of *S. aurita* in the catch. Even with these changes, there is essentially no change in the parameter values. Thus the estimated model appears to be robust to additional

years of data, even to data that are seemingly different from the previous years.

The estimated model for CPUE from the years 1966–80 is

$$\begin{aligned}\text{LNCPUE}(t) = {} & 0.248\cdot\text{LNCPUE}(t-1) \\ & + 0.254\cdot\text{LNCPUE}(t-2) \\ & + 0.162\cdot\text{LNCPUE}(t-4) \\ & + 0.143\cdot\text{LNCPUE}(t-24) \\ & - 0.143\cdot\text{SST}(t-1) \\ & + 0.112\cdot\text{SST}(t-2) \\ & + 0.044\cdot\text{SST}(t-17)\end{aligned}$$

where LNCPUE(t) = LN(CPUE(t) + 0.05) and t references the time period in fortnights. The model explains 43% of the observed variance in the data. Without the two outliers, the model explains almost 55% of the observed variance. Observed and one-step-ahead predicted values of CPUE transformed back to the original scale (Fig. 5) show that the predicted values are close to the observed values except at the large peaks in CPUE. Also, the predicted values are generally better before 1973 than after, which may be due to the problems in effort mentioned earlier. The model also frequently predicts the beginning and end of the fishing season (see for example 1968, 1974, 1979, and 1981).

A scatterplot of the observed CPUE versus the predicted CPUE (not shown) shows a trend to underpredict at high levels of CPUE, particularly at values greater than 12 tons per day. In the next section we will discuss some reasons for this observation.

Interpretation of the Model and Examination of the Form of the Relationship between CPUE and its Predictors

An empirically derived model is more satisfying if it has an interesting biological interpretation which is consistent with or combines previous observations on the fishery. The model estimated in the last section has such an interpretation. All else being equal, CPUE will show some persistence on its own; at low levels it will tend to remain low and higher levels will exponentially decline at a reasonable rate. If a "kick" comes that pushes CPUE up to a higher level, then the results of this "kick" will be felt for a few time periods to come. This may be due to schooling behavior. Conditions favorable for the formation of large schools tend to persist so that the schools themselves are available to the fishery for an extended period.

From the model estimates, what appears to provide the needed "kick" is a drop in SST from two fortnights ago to one fortnight ago. The sharper the drop in temperature and the longer the duration of the drop, the greater the effect on CPUE. If SST was relatively warm two fortnights ago and relatively warm one fortnight ago, there will not be much change in CPUE. Similarly, if SST was relatively cold two fortnights ago and relatively cold one fortnight ago, again there will not be much change. Once the increase is started, it will be maintained for a while by the persistence of CPUE noted above. Thus, it is not colder or warmer waters per se that are conducive to high levels of CPUE, but rather a long and sharp drop in temperature. This is of course the behavior of SST at the onset of the upwelling seasons. The model suggests that the beginnings and endings of fishing seasons should be related to upwelling and the success of the fishing season related to whether the season had strong or weak upwelling. Binet (1976) has presented results that show a correlation between a drop in SST and an increase in zooplankton biomass a fortnight later. Binet (1983) also has suggested that the colder waters tend to increase the aggregation of the zooplankton at the surface, and hence presumably to aggregate the fish as well. It is during the upwelling seasons with the onset of colder waters that we find higher levels of CPUE (Fig. 4e). As the fish species in our model feed on zooplankton (Dia 1972), this explanation of the physical mechanism underlying the model would appear to be consistent with independent biological observations.

E. Marchal (Antenne ORSTOM, Centre Oceanologique de Bretagne, Brest, pers. comm.) has suggested that CPUE lagged on itself at periods of 2, 4, 6, and 8 arises from the affect of the lunar cycle on these species noted in Marchal (1967). He also suggested that the residual correlation at lag 35 is approximately the correct lag at which the lunar and solar fortnights would be in phase. Thus, some of the long-term (four fortnights) persistence in CPUE may be due to this lunar effect.

So far we have restricted ourselves to linear models, with only a minor transformation in the CPUE data. There are a priori reasons to believe that the relationships between CPUE with itself lagged in time and between CPUE with SST at the various lags are nonlinear and that there may be possibly nonlinear transformations of the data that would improve the fit of the model while still maintaining an additive model which has better statistical properties. Plots of LNCPUE at time t versus SST at time t and $t-1$ (not shown) suggest a discontinuity or threshold in the relationship around approximately 27°C. These plots do not correct for the effect of the other variables in the model.

TABLE 4. Final estimates and estimated standard error of the parameters from time series analysis from 1966 to 1982 and 1966 to 1980 using the (a) seasonal cycle and (b) iterative algorithm to fill-in SST series.

Parameter		1966–82 Estimate	1966–82 SE	1966–80 Estimate	1966–80 SE
(a) Seasonal cycle					
Lag 1	LNCPUE	+0.258	0.047	+0.224	0.051
	SST	−0.143	0.039	−0.122	0.043
Lag 2	LNCPUE	+0.254	0.051	+0.223	0.054
	SST	+0.112	0.038	+0.090	0.042
Lag 4	LNCPUE	+0.162	0.048	+0.171	0.051
	SST	—	—	—	—
Lag 17	LNCPUE	—	—	—	—
	SST	+0.029	0.013	+0.045	0.013
Lag 24	LNCPUE	+0.144	0.042	+0.131	0.044
	SST	—	—	—	—
(b) Iterative algorithum					
Lag 1	LNCPUE	+0.261	0.047	+0.234	0.051
	SST	−0.141	0.043	−0.117	0.046
Lag 2	LNCPUE	+0.257	0.051	+0.227	0.054
	SST	+0.114	0.042	+0.089	0.045
Lag 4	LNCPUE	+0.159	0.048	+0.169	0.051
	SST	—	—	—	—
Lag 17	LNCPUE	—	—	—	—
	SST	+0.038	0.013	+0.042	0.014
Lag 24	LNCPUE	+0.148	0.042	+0.130	0.045
	SST	—	—	—	—

TABLE 5. Residual cross-correlations from lag 1 to 36 ("+" denotes a significant value and "−" a nonsignificant value at 5%).

Lag	CPUE	SST
1	−	−
2	−	−
3	−	−
4	−	−
5	−	−
6	−	−
7	−	−
8	−	−
9	−	−
10	−	−
11	−	−
12	−	−
13	−	−
14	+	−
15	−	−
16	−	−
17	−	−
18	−	−
19	−	−
20	−	−
21	−	−
22	−	−
23	−	−
24	−	−
25	−	−
26	−	−
27	−	−
28	−	−
29	−	+
30	−	−
31	−	−
32	−	−
33	−	−
34	−	−
35	+	−
36	−	−

To find "good" transformations of the data, we used a technique developed by Breiman and Friedman (1985) that empirically calculates optimal transformation of the data (see Appendix for further descriptions). The results of the algorithm are a smoothed empirical transformation of each of the observed data points. The implied functional form can be found by plotting the transformed value of the variable versus the original value. The transformed values are in no particular units (unless a functional transformation can be discerned from the plot; then the transformed data would be in whatever units are implied by that particular functional transformation).

In our model, the response variable is CPUE at time t, and the predictor variables are CPUE at times $t-1$, $t-2$, $t-4$, and $t-24$ and SST at times $t-1$, $t-2$, and $t-17$. The resulting transformed model explains 59% of the observed variance in the original series. It is worth emphasizing that this is not necessarily the optimal transformed model. We used the lags and parameters identified in our linear model as the correct ones. It is possible that if the correct transformations had been known a priori, then other lags of either CPUE or SST would have been found to be more important as predictors of CPUE at time t. Also, slightly different results are obtained for CPUE depending on which set of fill-ins is used for SST.

The optimal transformations for CPUE and for CPUE lagged one fortnight (not shown) range between a linear to a log transformation; the most noticeable difference from a log transformation is that the curve is less flat at high values of CPUE (>12). The results suggest that a slightly less steep transformation might have been preferable.

The transformation for CPUE lagged four fortnights (Fig. 6a) shows a sharp discontinuity in the relationship. The transformation is almost piecewise linear with a point of discontinuity around 12 tons per 24 h of search. Beyond this point, the value increases sharply. It does not seem coincidental that this is the same value at which we find our model consistently underpredicting CPUE. Our best guess is that this result has to do with schooling behavior of the fish: first that such behavior may influence our measure of effort, and hence influence CPUE (discussed earlier in the paper), and second that once either large schools are formed or perhaps many schools are formed, the fish become much easier to find so that CPUE sharply increases. Why the sharpest discontinuity should be at a lag of four fortnights is not obvious, but is clearly a topic for further study.

We would expect that the relationship between CPUE and SST would be nonlinear, probably some type of threshold function. This is because there are temperatures too high for the *Sardinella*, so an increase in SST above some given temperature will not affect CPUE significantly, and similarly there is also probably a temperature too low for the species. The transformation for SST at a lag of one fortnight (Fig. 7a) decreases linearly to 28°C, increases to 28.5°C, and then again sharply decreases. Not surprisingly, the sharpest response is between 27 and 28°C. The reason for the change in sign at 28°C is unclear, but it is clear that the linear relationship of the original model will only roughly approximate this functional form. The transformation of SST at a lag of two fortnights (Fig. 7b) displays the expected threshold effect; it linearly increases to just short of 28°C and then levels off. Further increases in SST will not affect CPUE further. Marchal (1967) studied 1 yr of data and found 23−26°C to be the optimal temperature range and reported a sharp drop in CPUE between 28 and 29°C. Our transformation clearly supports this finding and shows that it is valid for more than the single year Marchal studied.

The transformation for SST lagged 17 fortnights (Fig. 7c) is not as easily interpreted. It is highly nonlinear, almost bimodal in form. E. Marchal (pers. comm.) has suggested that the relationship with SST 17 fortnights earlier possibly may be due to the effect on an earlier life stage of the fish.

The transformations show that our simple linear models will be adequate over some of the range of the observed data, but that there are sharp discontinuities that will cause systematic bias in the predictions. These results also show that we can find additive models with all the variables transformed to a proper scale that remove most of the difficulties. The nonlinear form of the transformations do not alter on the whole the physical interpretation of our model: indeed, except for the effect of CPUE lagged four fortnights, it would seem to reinforce it. The transformation of CPUE lagged four fortnights may reflect schooling behavior and changes in school size and distribution because of the sharp nonlinearity in the transformation for values greater than 12 tons per day of searching. More accurate forecasts could probably be developed using measures of CPUE that better reflect both the spatial and size distribution of the schools and the number of boats searching.

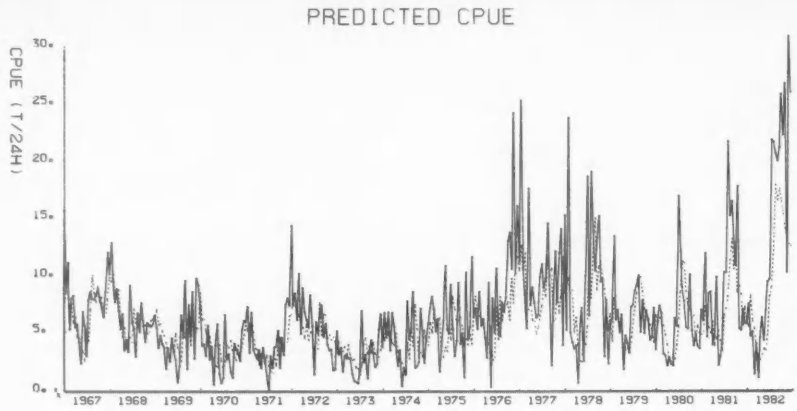


FIG. 5. Observed (solid line) versus predicted (broken line) CPUE from 1967 to 1982.

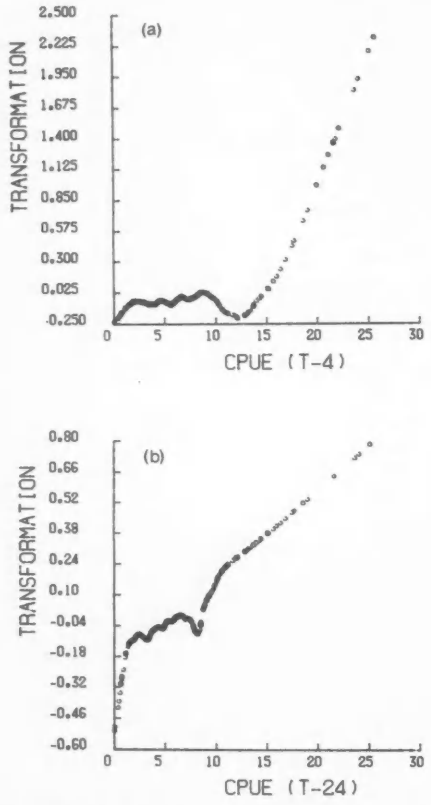


FIG. 6. Estimated optimal transformations of CPUE.

Forecasts

To test the ability of the model to forecast, the parameter values used were those estimated only from the data for the years 1966–80. The natural logarithm of CPUE was used in the forecasting model as discussed previously. The other transformations discussed in the previous section were not used in calculating the forecasts. Making use of these transformations to improve the forecasts is an area of future research. The estimated model then was used to produce one-step-ahead forecasts for the years 1981 and 1982 with no further reestimation of the parameters. This is similar to what might have been done at the end of 1980 if real-time data had been available, that is, if at the end of each fortnight we had been able to obtain the CPUE and SST data for that fortnight in order to produce the next period's forecast. With the present data collection system, real-time data are not available. However, real-time data could be made available, as SST is now collected through a satellite network, and catch and search data could be radioed in if the fishermen were willing to cooperate. Also, the real-time forecasts can be viewed as the best we can do; any delay in obtaining the data should only worsen the quality of the forecast.

As the model forecasts LNCPUE(t), we used the unbiased inverse transform (Granger and Newbold 1977, p. 307):

$$\text{CPUE}(t) = \exp\{\text{LNCPUE}(t) + 0.5 \cdot (\text{SE}) \cdot 2\}$$

where SE is the standard error of the forecast on the logarithmic scale.

The forecasts for the years 1981 and 1982 give a reasonable fit to the observed data (Fig. 8). The amplitude and duration of the seasonal fluctuations are reasonably described. In 1981, when there were real SST data, the increase in CPUE at the beginning of the main cold season was anticipated by the model's forecast. In 1982, the forecast trailed by one period and was partly brought up by the increase in CPUE itself. As noted earlier, the estimated seasonal cycle for SST was used in place of the missing data in these periods, and it is likely that the seasonal cycle did not successfully capture the onset of the upwelling season that year. The actual fishing success responded to a real decrease in temperature, while the filled in data contained no change in SST that would predict a rise in CPUE. Based on the results for 1981 and the predictions for other years where real data were available, there are justifiable reasons to believe that with the proper SST data the model would have forecasted an increase in CPUE.

The model did a reasonable job of predicting the very high peaks in CPUE in 1981 and especially in 1982. This is particularly surprising, since the catch in 1982 had a sharp increase in the percentage of *S. aurita* found in the catch. Although further testing would still be needed, it does appear that this

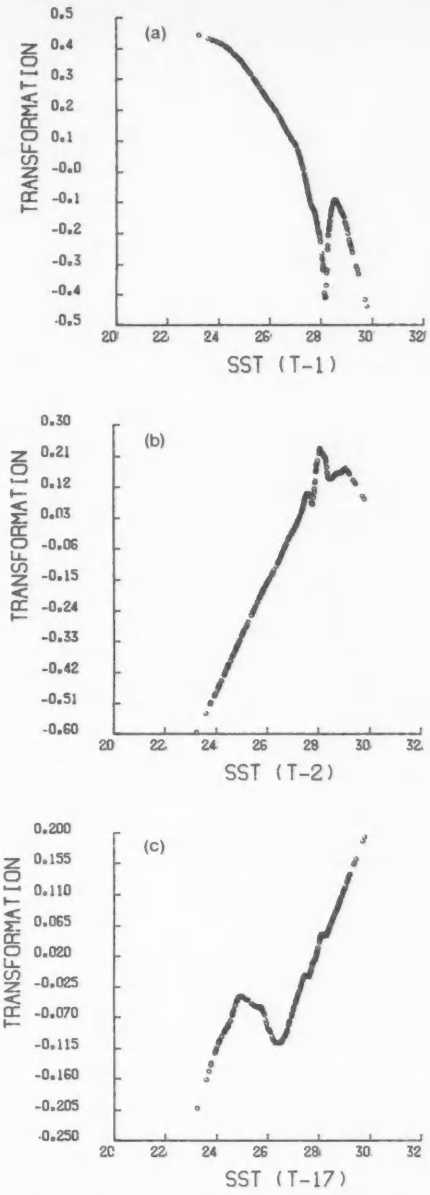


FIG. 7. Estimated optimal transformations of SST.

first-pass effort at modeling the dynamics could produce useful forecasts of the start and close of the fishing season and of the relative success in fishing that could be expected.

Discussion and Conclusions

The model estimated in this paper as well as the calculated transformations appear to provide a useful understanding of how the environment and past fishing success affect present fishing conditions. When good environmental data are available, the estimated model also provides a first-pass forecast that may be able to predict the start and close of fishing seasons and to predict catch rates during this period.

We have chosen to model the combined CPUE over all the species. There is a trade-off in this decision. With CPUE combined over all the species, it is not possible to interpret the results in terms of the dynamics of an individual species. Different species may react in different ways to environmental events so that the combined result may not reflect either species' behavior accurately.

On the other hand, CPUE combined over all species is more reflective of the situation as viewed by the fishermen. Also, it is not clear how to partition the effort between species, so that any species-specific measure of CPUE may have more problems than a CPUE combined over species. Further, it is likely that all the species feed on similar food sources and respond to an increase in food availability in a similar fashion. If the main influence of the environment is due to its affect on food availability, then CPUE combined over all species should be a very reasonable measure.

There are several features of the data that need to be checked. Some of the data were "filled in" using a smoothing algorithm, and it is not desirable to have these data points unduly influence the analysis. Also, in 1982 there was a sharp change in species composition, with *S. aurita*, a species associated with colder waters, increasing dramatically over the other species which apparently do not have as strong a temperature preference.

The filled in data appear to have had little influence on the model estimation, but they significantly affected the model fit and especially the model forecasts. The CPUE data have relatively few missing data points, and these points are for the most part randomly scattered throughout the data set. Thus, the filled in CPUE values probably affected the analysis little. SST data are missing almost the entire year of 1969 and the last half of 1982. However, an almost identical model is estimated whether the years 1981 and 1982 are included or not and for either method of filling in the missing SST values. So the estimated model appears to be robust to these fill-ins.

The predicted and forecasted values, particularly for the end of 1982, appear to be affected by the filled in data. This is not surprising, as the model looks for a sharp change in SST to produce a sharp change in CPUE; the seasonal cycle of SST may not accurately reflect the timing of the onset of upwelling in 1982.

At a fortnightly time scale, the measure of CPUE used probably reflects the availability of the pelagic stocks more than it reflects the year-to-year abundance of the stocks. As discussed earlier, the model predicts strong persistence in CPUE, so that once fish are present they tend to remain. The "kick" to increase appears to be associated with a drop in temperature from two fortnights ago to one fortnight ago. This appears to be consistent with upwelling periods. The transformations suggest a strong linear effect between 22 and 27°C and then a dropoff between 28 and 29°C. This is consistent with a study of Marchal (1967) on a single year's data where he found that 23–26°C was the optimum temperature range. Binet (1976) has shown that increases in zooplankton abundance occur one fortnight after a drop in temperature, and the increase in zooplankton is strongest following the onset of upwelling. This is consistent with the interpretation of our model. The pelagic species probably come to the surface more and school more when there is abundant zooplankton biomass around which to aggregate.

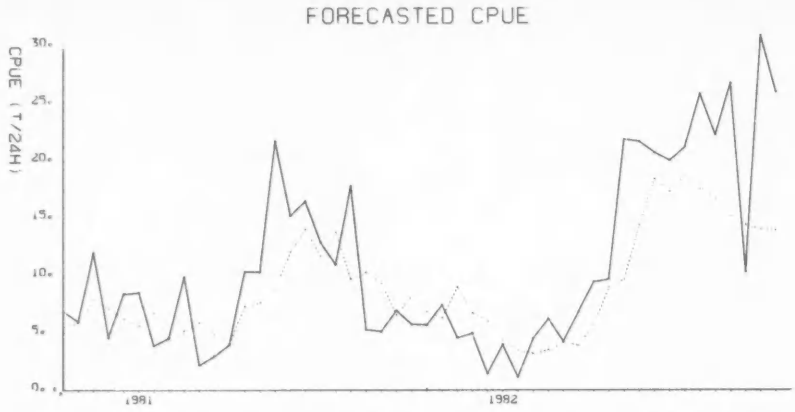


FIG. 8. Observed (solid line) and forecasted (broken line) CPUE in 1981 and 1982 per fortnight.

The CPUE of the coastal pelagic fish stocks off the Ivory Coast fluctuates greatly from one fortnight to another. Using mutivariate time series methods, a model has been constructed which explains 43% of the variance in the original series and provides reasonable forecasts of future data. The estimated model has a nice biological interpretation which is consistent with past studies on these species. By finding appropriate transformations of the original series, a model can be constructed which explains almost 60% of the total variance in the CPUE series. These transformations clarify the threshold and other nonlinear effects between CPUE and the environment.

The present results suggest that, by themselves, variables such as SST or salinity are not sufficient to explain the evolution of CPUE, particularly when measured at the same time period as the catch. Moreover, there are other environmental variables such as wind or subsurface data that were not available for our study but might also be important predictors of CPUE (Bakun and Parrish (1980) presented a list of likely environmental variables). Our results suggest that the measured environmental variables act as surrogate variables for oceanographic and biological processes that create favorable conditions for the targeted fish species. Therefore, it is the dynamics of these variables between periods that are important, not a static value at any one time period. A similar result was found by Mendelssohn and Roy (1986) for tuna in the Gulf of Guinea.

Finally, although our techniques are empirical, we have shown that they lend themselves to identifying the underlying processes involved. The modeling approach also avoids the problems of just examining cross-correlations, which are not independent of cross-correlations at other lags or of autocorrelations in either series. This can lead to spurious conclusions about relationships and the lags at which they occur. We have also used a new technique for identifying the appropriate scale or form of the relationships between the different variables under consideration.

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References

AKAIKE, H., G. KITAGAWA, E. ARAHATA, AND F. TADA. 1979. TIMSAC-78, Computer Science Monographs No. 11. The Institute of Statistical Mathematics, Tokyo. 279 p.

BAKUN, A., AND R. H. PARRISH. 1980. Environmental inputs to fishery population models for eastern boundary current regions, p. 67–104. *In* G. D. Sharp [ed.] Workshop on the effects of environmental variation on the survival of larval pelagic fishes. IOC Workshop Rep. 28.

BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. U.K. Minist. Agric. Fish Food. Fish. Invest. (Ser. 2) 19: 533 p.

BINET, D. 1976. Biovolumes et poids secs zooplanctoniques en relation avec le milieu pelagique au dessus du plateau ivoirien. Cah. ORSTOM Ser. Oceanogr. 14: 301–326.

1982. Influence des variations climatiques sur la pecherie des *Sardinella aurita* ivoiro-ghaneennes: relation secheresse-surpeche. Oceanol. Acta 5: 443–452.

1983. Zooplancton des regions cotieres a upwellings saisonniers du golfe de Guinee. Cah. ORSTOM Ser. Oceanogr. 18: 357–380.

BOUDREAULT, F. R., J. NORMAND DUPONT, AND C. SYLVAIN. 1977. Modeles linearies de prediction des debarquements de homard aux iles de la Madeleine (Golfe du Saint-Laurent). J. Fish. Res. Board Can. 34: 379–383.

BREIMAN, L., AND J. H. FRIEDMAN. 1985. Estimating optimal transformations for multiple regression and correlation. J. Am. Stat. Assoc. 80: 580–619.

CURY, P., AND C. ROY. 1985. Small pelagic fish abundance and upwelling off the Ivory Coast. Presented at UNESCO Symposium on vertical motions in the equatorial upper ocean and its effect upon living resources and the atmosphere, Paris, May 6–10.

DEMPSTER, A. P., N. M. LAIRD, AND D. B. RUBIN. 1977. Maximum likelihood from incomplete data via the EM algorithm. J. R. Stat. Soc. Ser. B 39: 1–38.

DIA, A. E. K. 1972. Etude de la nutrition de certains clupeides de Cote D'Ivoire. Projet de developpement de la peche pelagique cotiere, Ministere de la production animale. R/S 11/72: 33 p.

EBERHARDT, L. L. 1970. Correlation, regression, and density dependence. Ecology 51: 306–310.

FAO. 1974. Rapport terminal du projet FI: DP/IVC/66/506: Etude et mise en valeur des ressources en poissons pelagiques cotiers. Conclusions et recommandations. FAO, Rome. 72 p.

FONTENEAU, A., AND E. G. MARCHAL. 1970. Recolte, stockage et traitement des donnees statistiques relatives a la peche des sardiniers (filet tournant) en Cote D'Ivoire. Doc. Sci. C.R.O. Abidjan. 1: 21–30.

FOX, W. W. 1970. An exponential surplus yield model for optimizing exploited fish populations. Trans. Am. Fish. Soc. 99: 80–88.

GRANGER, C. W. J., AND P. NEWBOLD. 1977. Forecasting economic time series. Economic theory and mathematical economics series. Academic

Press, New York, NY. 333 p.
JENKINS, G. M. 1979. Practical experiences with modelling and forecasting time series. Time Series Library. Gwilym Jenkins & Partners (overseas) Ltd., Jersey, Channel Islands. 146 p.
MARCHAL, E. G. 1967. La peche des sardiniers ivoiriens en 1966. Doc. Sci. Prov. C.R.O. Abidjan. 19: 26 p.
MENDELSSOHN, R. 1981. Using Box–Jenkins models to forecast fishery dynamics: identification, estimation, and checking. Fish. Bull. 78: 887–896.
MENDELSSOHN, R., AND C. ROY. 1986. Environmental influences on the french, Ivory Coast, Senegalese and Moroccan tuna catches in the gulf of Guinea. *In* Special publication of the International Skipjack Year Program, ICCAT, Madrid.
MORLIERE, A. 1970. Les saisons marines devant Abidjan. Doc. Sci. C.R.O. Abidjan. 1: 1–15.
ORSTOM. 1976. Rapport du groupe de travail sur la sardinelle (*S. aurita*) des cotes ivoiro-ghaneennes. Fishery Research Unit Tema, Centre de Recherches Oceanographiques Abidjan, ORSTOM. 62 p.
PARRISH, R. H., A. BAKUN, D. M. HUSBY, AND C. S. NELSON. 1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction, p. 731–777. *In* G. D. Sharp and J. Csirke [ed.] Proceedings of the Expert Consultation to examine changes in abundance and species of neritic fish resources, Costa Rica, 18–29 April 1983. FAO Fish. Rep. 291.
PELLA, J. J., AND P. K. TOMLINSON. 1969. A generalized stock production model. Bull. IATTC 13: 419–496.
PICAUT, J. 1983. Propagation of the seasonal upwelling in the eastern equatorial Atlantic. J. Phys. Oceanog. 13: 18–37.
1985. Major dynamics affecting the eastern tropical Atlantic and Pacific oceans. Calif. Coop. Oceanic Fish. Invest. Rep. 26: 41–50.
RICKER, W. E. 1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Board Can. 119: 300 p.
SAILA, S. B., M. WIGBOUT, AND R. J. LERMIT. 1980. Comparison of some time series models for the analysis of fisheries data. J. Cons. Int. Explor. Mer 39: 44–52.
SCHAEFER, M. B. 1954. Some aspects of the dynamics of population important to the management of the commercial marine fisheries. Bull. Int. Am. Trop. Tuna Comm. 1: 26–56.
SHUMWAY, R. H., AND D. S. STOFFER. 1982. An approach to time series smoothing and forecasting using the EM algorithm. J. Time Ser. Anal. 3: 253–264.
TIAO, G. C., AND G. E. P. BOX. 1981. Modeling multiple time series with applications. J. Am. Stat. Assoc. 76: 802–816.
TIAO, G. C., G. E. P. BOX, M. R. GRUPE, G. B. HUDAK, W. R. BELL, AND I. CHANG. 1980. The Wisconsin multiple time series (WMTS-1) program. A preliminary guide. Department of Statistics, University of Wisconsin, Madison, WI. 75 p.

Appendix

Shumway–Stoffer Missing Data Algorithm

The Shumway–Stoffer (1982) missing data algorithm calculates maximum likelihood estimates of the parameters of the following state–space model:

$$x(t) = Ax(t-1) + e(t)$$
$$y(t) = Hx(t) + w(t)$$

where $x(t)$ is an underlying state of the system at time t, A is a matrix of parameters to be estimated relating the underlying state at time t to that at time $t-1$, $e(t)$ is the process error vector, $y(t)$ is the observed process at time t, H is a known matrix relating the underlying and observed processes, and $w(t)$ is a random vector, the observation error. The algorithm not only calculates maximum likelihood estimates of the parameters in the matrix A, but also calculates minimum mean-square error estimates of the underlying state $x(t)$, which is only observed with error in $y(t)$.

The algorithm has been extended to allow for missing data (i.e. missing components in the $y(t)$ vector), and the given reference shows how to put a multivariate autoregressive model into the required state–space form. The algorithm is a variant of the E–M algorithm of Dempster et al. (1977) and briefly proceeds as follows. For any estimate of the parameters, the algorithm uses a form of the Kalman filter to calculate the likelihood for that set of parameters. Minimum mean-square error estimates of the state vector $x(t)$ are then estimated using a slightly modified version of the Kalman fixed-interval smoothing algorithm. The new parameter estimates are then calculated by what is a regression-like equation. The next iteration then begins. The algorithm stops when the parameters have converged sufficiently.

For the applications in this paper, for example, the vector $y(t)$ is the observed CPUE in areas 4–7, the underlying state $x(t)$ is the "true" CPUE or density in areas 4–7 and the matrix A contains the parameters of a second-order autoregressive process. For the SST data, a second-order autoregressive process was estimated for each pair of bordering north–south areas.

Alternating Conditional Expectation (ACE) Algorithm

The ACE algorithm of Breiman and Friedman (1985) is an algorithm that estimates optimal transformations of variables in regression-like equations. The algorithm operates on the observation that for any given empirical transformations of the data, if we fix the values of all but one variable and solve the problem of what new transformation will minimize the normalized residual sum-of-squares, then the solution is a conditional expectation that can be empirically estimated using a smoothing algorithm.

The algorithm starts with the given variables and then alternately estimates the conditional expectations that would be derived from fixing all but one variable in turn. Hence, the name of the algorithm. The algorithm terminates when the changes in the estimated transformations are sufficiently small. The algorithm does not produce a given equation, but rather an empirical transformation of each data point for each variable. The shape of the transformation is found by plotting the transformed values of a variable versus the original values.

A Length-Based Stock Assessment Method Utilizing a Generalized Delay-Difference Model

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Fournier, D. A., and I. J. Doonan. 1987. A length-based stock assessment method utilizing a generalized delay-difference model. Can. J. Fish. Aquat. Sci. 44: 422–437.

We present a length-based stock assessment method based on a generalization of the delay-difference methods of Deriso. Data inputs to the model include the estimated weight of the catch, the estimated fishing effort, the estimated mean weight of the catch, and the estimated central moments of the length distribution of the catch. The model's performance is demonstrated by applying it to data from a simulated exploited fish population exhibiting biomass-dependent catchability which would cause conventional catch–effort models to seriously underestimate the extent of stock depletion. The model was generally able to detect the presence of the biomass-dependent catchability and to correctly estimate the optimal level of fishing effort.

Les auteurs présentent une méthode d'évaluation du stock basée sur la longueur d'après une généralisation des méthodes de différence du décalage de Deriso. Les données utilisées pour l'élaboration du modèle comprennent les estimations du poids des prises, de l'effort de pêche, du poids moyen des prises et des moments centrés de la distribution des longueurs dans les prises. On obtient un aperçu du rendement du modèle en l'appliquant à des données obtenues d'une population hypothétique exploitée de poissons qui montre un potentiel de capture dépendant de la biomasse; dans le cas des modèles conventionnels sur les prises et l'effort, ce dernier facteur sous-estimerait fortement l'importance de l'appauvrissement du stock. En général, le modèle pouvait déceler la présence du potentiel de capture dépendant de la biomasse et estimer précisément le niveau optimum d'effort de pêche.

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Deriso (1980) introduced a population dynamics model, based on concepts of age-structured populations, which had dynamical equations describing the evolution of the population over time that were independent of the age structure. This enabled the population dynamics to be described in terms of biologically meaningful parameters determining such things as growth, mortality, and the relationship between stock and recruitment while avoiding the necessity for specifying exactly what the numbers at age in the population were at any time.

While Deriso's approach represents a great conceptual advance over stock–production models such as Schaefer's model (Schaefer 1954; Schnute 1977), or generalizations thereof (Pella and Tomlinson 1969), its usefulness in practice has been hampered by the fact that while his model has considerably more parameters to estimate than stock–production models, it uses about the same amount of data, e.g. a time series of catch and effort data, to estimate these parameters. To overcome this difficulty, we shall demonstrate how Deriso's approach can be extended so that it will predict the values of other statistics easily collected with catch data, such as the mean length and weight of the catch, and the higher sampling moments of the length distribution of the catch. This approach increases the number of observations to be fitted by the model at the cost of introducing only a small number of additional parameters. It also produces a model which is a natural tool for length-based stock assessment.

To estimate the parameters in the model, we have adopted a Bayesian approach. This approach enables the user of the model to include prior knowledge or opinion into the analysis and to incorporate at the outset an optimistic or conservative view of the ability of the stock to withstand exploitation.

In keeping with this Bayesian viewpoint, parameterizations of relationships have been incorporated into the model even though they may not be well determined by the data alone. For example, the model utilizes a general form of stock–recruitment relationship which includes both the Ricker and Beverton–Holt stock–recruitment relationships as special cases.

To introduce the methods used in the paper in the simplest fashion, we have begun with the one group case considered by Deriso. The difference equations satisfied by the biomass of the population and the total number of fish in the population are derived.

The main part of the paper deals with the extra complexity brought about by the incorporation of length data, multiple fisheries, and age-dependent effects into the model.

A good criterion justifying the introduction of a complicated new theory and a model resulting from it would be that one must demonstrate that situations might reasonably exist where the complicated model can produce a better analysis than simple alternative models. Ludwig and Walters (1985) showed

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that a very simple model could outperform Deriso's model for simulated data where the data were generated according to Deriso's model's hypotheses. It would seem therefore that Deriso's model itself has already failed this criterion and one might ask why an even more complicated model should be expected to perform better.

Both Deriso's model and Ludwig and Walter's model (which appeared originally in Ludwig and Hilborn 1983) assume that there is constant catchability, i.e. that a simple relationship such as

$$C_i = B_i(1 - \exp(-q\hat{E}_i))$$

holds in the ith year where C_i is the catch in year i, B_i is the biomass in year i, $\hat{E}_i$ is the estimated fishing effort in year i, and q is the constant catchability.

The use of constant catchability has been criticized on the grounds that the behavior of some species, especially schooling behavior (Clark and Mangel 1979), may result in catchability increasing as the biomass is reduced by exploitation. Such an effect can have important management implications.

The reason that the constant catchability assmption is made in models which utilize only catch and effort data is that there is not enough information in such data to determine whether the catchability is biomass dependent or not. To date, the only methods which can investigate the relationship between biomass and catchability involve the use of data derived by aging the fish, or by using age estimates produced by using an age–length relationship. Aging data are difficult and expensive to obtain. Age–length relationships only produce useful age estimates when the relationship is known with sufficient accuracy and when the length distributions of neighboring age classes do not overlap too much. An alternative method which used length data from a fishery directly, without the need to impute ages to the fish and which could detect biomass-dependent changes in catchability, could be very useful.

To demonstrate the model's ability to analyze fisheries data without the need for age data and without the necessity for making the constant catchability hypothesis, an approach similar to that of Ludwig and Walters (1985) was used. A series of simulated data sets were generated and analyzed and the results used to estimate the optimal level of effort. The main extension to the assumptions adopted by Ludwig and Walters was the inclusion of a biomass-dependent effect in the catchability. This effect would lead to a severe underestimation of the extent of stock depletion if it were not accounted for. The model was generally able to detect the biomass-dependent component of the catchability and correctly determine the optimal level of exploitation.

Simplest Case

The general model contains a large number of concepts and this may obscure the main ideas. For this reason we first present a less formal discussion of the necessary ideas in the simplest case.

To avoid the introduction of an excessive amount of notation we shall introduce notation in this section which has a slightly different interpretation from that used in the rest of the paper.

Notation

i indexes the fishing year
j indexes the ages
N_{ij} total number of fish of age j at the beginning of year i
$N_{i\cdot}$ total number of fish in year i
R_i recruitment in year i (in numbers of fish)
l survival rate (from natural mortality)
s_i survival rate from fishing in year i
C_i total weight of the catch in year i
$\hat{C}_i$ estimated total weight of the catch in year i
M_i mean weight of the fish in the population in year i
$\hat{M}_i$ estimated mean weight of the fish in the population in year i.
w_j mean weight of an age j fish
ρ Brody growth coefficient
B_i total weight of the fish in the population in year i
k age at which the fish recruit to the population
q catchability in the effort – fishing mortality relationship
E_i effect fishing effort in year i
$\hat{E}_i$ estimated fishing effort in year i

We assume that there is a lag of k years before the fish recruit. After recruitment all fish are assumed to be equally vulnerable to the fishery regardless of their ages. For simplicity assume that the fishery takes place at the beginning of the year over a time period so short that natural mortality can be ignored. Let s_i denote the survival rate from fishing and l the survival rate from natural mortality. Then $(1 - s_i)$ is the proportion of fish caught in the fishery.

Assume that the stock dynamics of the population are given by the equations

$$N_{ik} = R_i \tag{1.1}$$

and for $j > k$

$$N_{ij} = l\, s_{i-1} N_{i-1,j-1}. \tag{1.2}$$

The simplest difference equation is satisfied by the total number of fish in the population denoted by $N_{i\cdot}$:

$$N_{i\cdot} = \sum_{j \geq k} N_{ij}. \tag{1.3}$$

In expression 1.3, split off the first term to obtain the equivalent expression

$$N_{i\cdot} = \sum_{j>k} N_{ij} + R_i \tag{1.4}$$

or by expression 1.2

$$N_{i\cdot} = l s_{i-1} \sum_{j \geq k} N_{i-1,j} + R_i$$

or

$$N_{i\cdot} = l s_{i-1} N_{i-1,\cdot} + R_i. \tag{1.5}$$

Expression 1.5 is a first-order difference equation satisfied by the $N_{i\cdot}$. By employing expression 1.5 iteratively it is possible to express any $N_{i\cdot}$ in terms of the recruitments R_p for $2 \leq p \leq i$, the survival rates from fishing s_p for $1 \leq p \leq i-1$, the survival rate from natural mortality l, and the total number of fish in the population in year 1, $N_{1\cdot}$. For example, consider $N_{3\cdot}$:

$$N_{3\cdot} = l s_2 N_{2\cdot} + R_3$$

or

$$N_{3\cdot} = l s_2 (l s_1 N_{1\cdot} + R_2) + R_3. \tag{1.6}$$

Assume that w_j, the mean weight at age j of the fish, satisfies the relationship

$$(1.7)\quad w_j = a\left(\frac{1-\rho^j}{1-\rho}\right)\quad 0<\rho<1$$

where a is the mean weight of an age 1 fish.

It is easily verified that the w_j satisfy the first-order difference equation

$$(1.8)\quad w_j - \rho w_{j-1} = a.$$

The biomass in year i, B_i, is given by

$$(1.9)\quad B_i = \sum_{j\geq k} w_j N_{ij}.$$

The relationship 1.8 implies that

$$\sum_{j\geq k}(w_j - \rho w_{j-1})\, N_{ij} = aN_{i\cdot}$$

or

$$(1.10)\quad B_i = \rho \sum_{j\geq k} w_{j-1}N_{ij} + aN_{i\cdot}.$$

Using expression 1.2, one obtains

$$(1.11)\quad \sum_{j\geq k} w_{j-1}N_{ij} = ls_{i-1}\sum_{j\geq k} w_j N_{i-1,j} + w_{k-1}R_i.$$

Substituting the relationship 1.11 into expression 1.10 yields

$$(1.12)\quad B_i = \rho l s_{i-1}B_{i-1} + aN_{i\cdot} + \rho w_{k-1}R_i.$$

Expression 1.12 shows that the B_i also satisfy a first-order difference equation independent of the age structure. Since in expression 1.12 the B_i also depend on the $N_{i\cdot}$, the two expressions 1.5 and 1.12 together form a first-order system of difference equations.

Note that the derivation of the difference equation 1.12 satisfied by the B_i depended on the fact that the coefficients themselves satisfied the difference equation 1.8. This enabled the B_i to be expressed in terms of the $N_{i\cdot}$ and the "lagged" term

$$(1.13)\quad \sum_{j\geq k} w_{j-1}N_{ij}.$$

Expression 1.13 is not of the same type as B_i but it would be if the index j in N_{ij} matched the index $j-1$ in w_{j-1}. The relationships 1.1 and 1.2 enable this to be done. This is the general approach which is used to derive the desired difference equations in this paper.

To see how the above results could be used in practice, assume that for some fishery one has estimates of the total catch, the total fishing effort, and the mean weight of the catch for each year of the fishery. Let $\hat{C}_i$, $\hat{E}_i$, and $\hat{M}_i$ denote the values of these estimates for year i. Assume also that the survival rate s_i satisfies the relationship

$$(1.14)\quad s_i = \exp(-qE_i)$$

where q is an unknown parameter, the catchability. Since all fish are assumed to be equally vulnerable to the fishery, we shall assume that the total catches C_i satisfy the relationship

$$(1.15)\quad C_i = (1 - s_i)\, B_i.$$

For the recruitment R_i, we shall assume that a Ricker stock–recruitment relationship holds so that

$$(1.16)\quad R_{i+k} = \alpha B_i \exp(-\beta B_i).$$

Note that the recruitment cannot be calculated for the years 1 through k because corresponding biomass is not known. We shall deal with this problem by using the biomass B_1 in expression 1.16 to compute the R_i for $2 \leq i \leq k+1$.

For a given value of the parameters B_1, $N_{1\cdot}$, l, q, α, β, a, ρ, and the s_p, $1 \leq p \leq i-1$, it is possible to use equations 1.5 and 1.12 to calculate the quantities B_i and $N_{i\cdot}$ for all the years of the fishery. The mean weight M_i of the fish in the population can then be calculated from the relationship

$$(1.17)\quad M_i = B_i/N_{i\cdot}.$$

The method used for calculating the s_i, C_i, and E_i depends on the assumptions made about the form of the errors present in the data. If it is assumed that the estimated effort $\hat{E}_i$ is equal to the effective effort E_i, while the errors are in the observed catches, then the s_i can be calculated from 1.14 with E_i set equal to $\hat{E}_i$ and then the catches C_i calculated from 1.15 so that

$$s_i = \exp(-q\hat{E}_i)$$

and

$$C_i = (1 - \exp(-q\hat{E}_i))\, B_i.$$

If it is assumed that the true catches are equal to the estimated catches and the errors are in the estimated fishing effort, then the s_i can be calculated from 1.15 with C_i set equal to $\hat{C}_i$ giving

$$s_i = 1 - \hat{C}_i/B_i$$

and from the relationship 1.14

$$E_i = -\log_e(s_i)/q.$$

Finally, if it is assumed that there are errors both in the estimated catches and the estimated effort, then the effective efforts E_i become independent model parameters and the C_i and s_i are calculated from expressions 1.14 and 1.15.

Since all fish in the population are assumed to be equally vulnerable (after recruitment), the mean weight of the fish in the population is also the mean weight of the fish in the catch. To estimate the correct values of the model parameters, we pick those values of the model parameters for which the predicted values of the C_i, M_i, and E_i agree best with their observed values $\hat{C}_i$, $\hat{M}_i$, and $\hat{E}_i$.

Of course, the notion of best agreement depends on which criterion for measuring closeness is chosen. This criterion will depend on the type of probabilistic mechanisms which are assumed to generate the observations. One could assume, for example, that there is no error in the estimated effort so that $E_i = \hat{E}_i$ and that the observed catches are lognormally distributed and that the quantities $\log_e(\hat{C}_i)$ are normally distributed with means $\log_e(C_i)$, while the $\hat{M}_i$ are normally distributed with means M_i. Then the maximum likelihood criterion for closeness would be to pick that value of the parameters B_1, $N_{1\cdot}$, l, q, α, β, a, and ρ for which the sum of squares

$$(1.18)\quad \sum_i (\log_e(C_i) - \log_e(\hat{C}_i))^2 + p\sum_i (M_i - \hat{M}_i)^2$$

is minimized. The quantity p in expression 1.18 is a penalty weight which determines the extent to which the model attempts to fit the observed catches or the observed mean weights. In general, there is not enough information in the data to determine the correct value of p. Such information must be supplied from external sources or the desired value of p deter-

mined by external considerations. This sort of ambiguity is common in this type of model where different types of data, in this case total catch and mean weight data, are being combined. However, a general statement can be made.

If we regard the catch data $\hat{C}_i$ as the primary data and the mean weight data $\hat{M}_i$ as data supplying auxiliary information, then p would be set small enough so that the requirement of the model to fit the observed mean weight data would not prevent it from fitting the observed catch data.

Alternatively, one could assume that there is no error in the catch estimates so that $C_i = \hat{C}_i$ and that the estimated effort is lognormally distributed with the mean value of $\log_e(\hat{E}_i)$ equal to $\log_e(E_i)$. Then the maximum likelihood criterion for closeness would be to minimize the sum of squares

$$(1.19) \quad \sum_i (\log_e(E_i) - \log_e(\hat{E}_i))^2 + p \sum_i (M_i - \hat{M}_i)^2.$$

The simple model may be adequate for many purposes but it has several limitations. Because all the fish in the population are equally vulnerable to fishing, the model is not suitable for fisheries in which recruitment occurs gradually over time. Also, many fish populations are exploited by several fisheries where each fishery has its own age-dependent pattern of selectivity. It is desirable to develop a theory which allows for this level of complexity. Finally, with the assumed mean weight at age relationship 1.7, it is impossible to incorporate length data into the model while at the same time retaining a realistic weight–length relationship. The general model is intended to overcome these limitations.

General Model

To describe the general model, we introduce the following notation which will be used throughout the rest of the paper.

Notation

i indexes the fishing year
I total number of years of fishing
j indexes the age classes
f indexes the fisheries
N_f total number of fisheries
g indexes the groups the fish belong to
N_{ijg} = number of age j fish in group g at the beginning of year i
w_j = mean weight of an age j fish
R_i = recruitment in year i
B_{ig} = biomass of fish in group g at the beginning of year i
t_{fig} = proportion of the fish removed by fishing from group g caught by fishery f in year i
s_{ig} = survival rate (from fishing) for fish in group g in year i
l_g = survival rate (from natural mortality) in group g
τ_j = mean length of an age j fish
m_g = probability that a fish in group g remains in group g for another year
q_{fig} = catchability for group g in fishery f in year i
a = mean weight of the age 1 fish
ρ = Brody growth coefficient
b = coefficients in the weight–length relationship
RB_i = reproductive biomass in year i
Q_{f1g} = constant component of the catchability
Q_{f2g} = biomass-dependent component of the catchability
C_{fi} = weight of the catch in fishery f in year i
$\hat{C}_{fi}$ = estimated weight of the catch in fishery f in year i
n_{fi} = number of fish sampled for weight and length data from fishery f in year i
M_{fi} = mean weight of the catch in fishery f in year i
$\hat{M}_{fi}$ = mean weight of the fish in the random sample of the catch in fishery f in year i
M^2_{fi} = second central moment of the distribution of the weight of the catch for fishery f in year i from fishery f in year i
M_{fi} = mean weight of the catch in fishery f in year i
$\hat{M}_{fi}$ = mean weight of the fish in the random sample of the catch in fishery f in year i
M^2_{fi} = second central moment of the distribution of the weight of the catch for fishery f in year i
μ^r_{fi} = rth central moment of the lengths of the fish in the catch from fishery f in year i
$\hat{\mu}^r_{fi}$ = rth central moment of the lengths of the fish in the random sample of the catch from fishery f in year i
E_{fi} = (effective) fishing effort in fishery f in year i
$\hat{E}_{fi}$ = estimated fishing effort in fishery f in year i
σ^2_E = variance in the stochastic component of the relationship between estimated fishing effort and effective fishing effort
σ^2_R = variance in the stochastic component of the stock recruitment relationship
σ^2_L = variance in the distribution of the lengths of the fish in each age class around their mean

Data

Assume that there is a fish population which has been exploited by a number of fisheries for several years. Each fishery has its own age-dependent selectivity pattern. For simplicity we assume that all the fisheries occur simultaneously for a short period at the beginning of each year. (Short in this context means that mortality during the fishing period from causes other than fishing can be ignored.) We assume that for each year and fishery there are estimates of the total weight of the catch $\hat{C}_{fi}$ and the total fishing effort $\hat{E}_{fi}$. In addition a random sample of n_{fi} fish has been taken from each catch and the weight and length of each fish noted. (It is not necessary that the weight and length data come from the same sample. This assumption is only made for simplicity.) Let $\hat{M}_{fi}$ and $\hat{\mu}^1_{fi}$ denote the mean weights and mean lengths of the samples and $\hat{\mu}^2_{fi}$, $\hat{\mu}^3_{fi}$, and $\hat{\mu}^4_{fi}$ denote the second, third, and fourth central moments of the length distributions of the samples. To calculate the $\hat{M}_{fi}$ and $\hat{\mu}^r_{fi}$, let x_{fiy} and z_{fiy} denote the length and weight of the yth fish taken from fishery f in year i. Then

$$\hat{M}_{fi} = \frac{1}{n_{fi}} \sum_{y=1}^{n_{fi}} z_{fiy}$$

and

$$\hat{\mu}^1_{fi} = \frac{1}{n_{fi}} \sum_{y=1}^{n_{fi}} x_{fiy}$$

while for $r > 1$

$$\hat{\mu}^r_{fi} = \frac{1}{n_{fi}} \sum_{y=1}^{n_{fi}} (x_{fiy} - \hat{\mu}^1_{fi})^r.$$

The observations $\hat{C}_{fi}$, $\hat{E}_{fi}$, $\hat{M}_{fi}$, and $\hat{\mu}^r_{fi}$, $r = 1, 2, \ldots, 4$, are the data which will be used in the model. The $\hat{M}_{fi}$ and $\hat{\mu}^r_{fi}$ are random variables. Let $M_{fi} = E\{\hat{M}_{fi}\}$ and $\mu^r_{fi} = E\{\hat{\mu}^r_{fi}\}$ denote

the expected value of these random variables. Let C_{fi} denote the actual weight of the catch.

Fitting the Model

Assume for the moment that the system of difference equations has been derived so that the quantities C_{fi}, E_{fi}, M_{fi}, and the μ^r_{fi} can be expressed in terms of a (relatively) small number of model parameters. We shall denote the set of all model parameters by Θ. (The exact number and form of the model parameters will vary in different applications, so we wish to refer to them in a generic fashion at this point.)

The proper method to fit the model depends on the form of the probabilistic assumptions which are made. It will be assumed that the $\hat{M}_{fi}$ are normally distributed with mean M_{fi} and variance v_1^2 and that the $\hat{\mu}^r_{fi}$, $r = 1, \ldots, 4$, are normally distributed with means μ^r_{fi} and variances v^2_{r+1}.

Since the sample moments $\hat{M}_{fi}$ and the $\hat{\mu}^r_{fi}$ are asymptotically normally distributed, the assumption that they are normally distributed is fine as long as the sample sizes n_{fi} are large enough, and this assumption did not appear to cause any problems with the results from the simulations. However, if the length distribution of the catch is highly skewed, or the sample sizes are small, the distribution of the third and fourth sample moments may also be highly skewed. The higher sampling moments are also extremely sensitive to outliers in the data. For these reasons it may be advantageous to employ statistics with better statistical properties than the higher sampling moments and to fit them by procedures which are more robust than least squares.

A simple alternative to using the third and fourth sample moments of the catch would be to use the sample skewness $\hat{\mu}^3_{fi}/(\hat{\mu}^2_{fi})^{1.5}$ and the sample kurtosis $\hat{\mu}^4_{fi}/(\hat{\mu}^2_{fi})^2$.

With respect to the observed catches $\hat{C}_{fi}$ and estimated efforts $\hat{E}_{fi}$, two approaches are commonly used. The first is to assume that the effective fishing effort E_{fi} is equal to the estimated fishing effort $\hat{E}_{fi}$ and that all the error is between the observed catches $\hat{C}_{fi}$ and the true catches C_{fi}. The $\hat{C}_{fi}$ are assumed to be lognormally distributed and $\log_e(\hat{C}_{fi})$ is assumed to be normally distributed with mean $\log_e(C_{fi})$ and variance v_0^2. The second approach is to assume that the estimated efforts $\hat{E}_{fi}$ are lognormally distributed and that $\log_e(\hat{E}_{fi})$ is normally distributed with mean $\log_e(E_{fi})$ and variance v_6^2.

The second approach is probably more realistic in that there is likely to be a large component of variability in the relationship between estimated fishing effort and the resulting fishing mortality, while the catch can be well estimated at least in principle by using good fleet sampling schemes. The implementation of the second approach in the general model involves considerable technical difficulties, however, so we shall forego further discussion of it until later.

Let $V = (v_0^2, v_1^2, \ldots, v_5^2)$ denote the vector of variance parameters.

With the first approach the log-likelihood function $F(\Theta, V)$ for the parameters is given by

$$(2.1)\quad F(\Theta, V) = -\sum_{fi}\{\log_e(C_{fi}(\Theta)) - \log_e(\hat{C}_{fi})\}^2/v_0^2 - \sum_{fi}\{M_{fi}(\Theta) - \hat{M}_{fi}\}^2/v_1^2 - \sum_{fi}\{\mu^1_{fi}(\Theta) - \hat{\mu}^1_{fi}\}^2/v_2^2 - \sum_{fi}\{\mu^2_{fi}(\Theta) - \hat{\mu}^2_{fi}\}^2/v_3^2 - \sum_{fi}\{\mu^3_{fi}(\Theta) - \hat{\mu}^3_{fi}\}^2/v_4^2 - \sum_{fi}\{\mu^4_{fi}(\Theta) - \hat{\mu}^4_{fi}\}^2/v_5^2 - \sum_{fi}\sum_{u=0}^{5}\log_e(v_u).$$

In expression 2.1 the parameter v_0^2 is the variance of the random variables $\log_e(\hat{C}_{fi})$. The terms v_1^2 through v_5^2 are the variances of the corresponding sample moments. There are many different structural assumptions that can be made about the variance parameters V. The form of the assumption made depends on how much is assumed to be known, a priori, about these parameters. We shall describe three such assumptions here. They include those assumptions which assume the most a priori knowledge and the least a priori knowledge about these parameters.

The terms v_0^2 through v_5^2 can either be assumed to be known, assumed to be known up to a multiple of each other, or be estimated. The maximum likelihood estimates for the parameters would be found by maximizing expression 2.1 with respect to Θ and V. The estimates obtained depend on the form of the structural assumptions made about V.

Rather than adopting this approach, we have chosen a Bayesian approach which involves the addition of an extra term to the log-likelihood function.

Because some of the parameters in the model such as the growth determining coefficient ρ, the natural survival rates l_g, and the mean length of the fish at the age of recruitment have an interpretation independent of the model, there will often be information about them besides that contained in the data. This additional information is included in the model by assuming the existence of a probability distribution on these parameters whose probability density function is denoted by $G(\Theta)$. The logarithm of the posterior probability distribution for the parameters is given by

$$(2.2)\quad \Phi(\Theta, V) = F(\Theta, V) + \log_e(G(\Theta)).$$

The mode of the posterior distribution is given by those values of the parameters Θ and V which maximize 2.2. These parameter estimates have been used in the estimation and formulation of the optimal policy in the simulation examples.

The values of the parameters obtained when maximizing 2.2 will depend on which of the three assumptions about the parameters V is used. Each assumption has its advantages and disadvantages.

Since $G(\Theta)$ does not depend on V, to maximize expression 2.2 with respect to V, it suffices to first maximize expression 2.1 with respect to V and to substitute the resulting expression $\tilde{F}(\Theta)$ which does not depend on V into 2.2.

Case 1. The v's are assumed known and fixed

In this case the term

$$\sum_{fi}\sum_{u=0}^{5}\log_e(v_u)$$

is constant and can be ignored. Then

$$(2.3)\quad \tilde{F}(\Theta) = -\sum_{fi}\{\log_e(C_{fi}(\Theta)) - \log_e(\hat{C}_{fi})\}^2/v_0^2$$

$$- \sum_{fi} \{M_{fi}(\Theta) - \hat{M}_{fi}\}^2/v_1^2$$

$$- \sum_{fi} \{\mu_{fi}^1(\Theta) - \hat{\mu}_{fi}^1\}^2/v_2^2$$

$$- \sum_{fi} \{\mu_{fi}^2(\Theta) - \hat{\mu}_{fi}^2\}^2/v_3^2$$

$$- \sum_{fi} \{\mu_{fi}^3(\Theta) - \hat{\mu}_{fi}^3\}^2/v_4^2$$

$$- \sum_{fi} \{\mu_{fi}^4(\Theta) - \hat{\mu}_{fi}^4\}^2/v_5^2$$

where in expression 2.3 the v's are known constants.

Case 2. The v's are known multiples of each other

Assume that

$$(2.4) \quad p_i = v_0^2/v_i^2$$

where the p_i are assumed to be known. Then expression 2.1 can be rewritten as

$$(2.5) \quad F(\Theta, V) = - p_0 \sum_{fi} \{\log_e(C_{fi}(\Theta)) - \log_e(\hat{C}_{fi})\}^2/v_0^2$$

$$- p_1 \sum_{fi} \{M_{fi}(\Theta) - \hat{M}_{fi}\}/v_0^2$$

$$- p_2 \sum_{fi} \{\mu_{fi}^1(\Theta) - \hat{\mu}_{fi}^1\}/v_0^2$$

$$- p_3 \sum_{fi} \{\mu_{fi}^2(\Theta) - \hat{\mu}_{fi}^2\}/v_0^2$$

$$- p_4 \sum_{fi} \{\mu_{fi}^3(\Theta) - \hat{\mu}_{fi}^3\}/v_0^2$$

$$- p_5 \sum_{fi} \{\mu_{fi}^4(\Theta) - \hat{\mu}_{fi}^4\}/v_0^2$$

$$- 6 \sum_{fi} \log_e(v_0)$$

$$+ \sum_{fi} \sum_{u=0}^{5} \log_e(p_u)/2.$$

In expression 2.5 a term p_0 has been included. This term would normally have the value of 1. It has been included so that the catch data can be given a greater weight when fitting the model if this is desired by giving p_0 a value larger than 1.

The value of v_0 maximizing expression 2.5 satisfies the condition

$$(2.6) \quad \partial F(\Theta, V)/\partial v_0 = 0.$$

Differentiating expression 2.5 with respect to v_0 and solving the equation 2.6 for v_0 yields

$$(2.7) \quad v_0^2 = [p_0 \sum_{fi} \{\log_e(C_{fi}(\Theta)) - \log_e(\hat{C}_{fi})\}^2$$

$$+ p_1 \sum_{fi} \{M_{fi}(\Theta) - \hat{M}_{fi}\}^2$$

$$+ p_2 \sum_{fi} \{\mu_{fi}^1(\Theta) - \hat{\mu}_{fi}^1\}^2$$

$$+ p_3 \sum_{fi} \{\mu_{fi}^2(\Theta) - \hat{\mu}_{fi}^2\}^2$$

$$+ p_4 \sum_{fi} \{\mu_{fi}^3(\Theta) - \hat{\mu}_{fi}^3\}^2$$

$$+ p_5 \sum_{fi} \{\mu_{fi}^4(\Theta) - \hat{\mu}_{fi}^4\}^2]/IN_f.$$

Substituting this expression for v_0^2 into 2.5 and discarding the constant terms (which are irrelevant for the maximization) yields

$$(2.8) \quad \tilde{F}(\Theta) = -\log_e [p_0 \sum_{fi} \{\log_e(C_{fi}(\Theta)) - \log_e(\hat{C}_{fi})\}^2$$

$$+ p_1 \sum_{fi} \{M_{fi}(\Theta) - \hat{M}_{fi}\}^2$$

$$+ p_2 \sum_{fi} \{\mu_{fi}^1(\Theta) - \hat{\mu}_{fi}^1\}^2$$

$$+ p_3 \sum_{fi} \{\mu_{fi}^2(\Theta) - \hat{\mu}_{fi}^2\}^2$$

$$+ p_4 \sum_{fi} \{\mu_{fi}^3(\Theta) - \hat{\mu}_{fi}^3\}^2$$

$$+ p_5 \sum_{fi} \{\mu_{fi}^4(\Theta) - \hat{\mu}_{fi}^4\}^2]/2.$$

Case 3. All the v's estimated

In this case, solving the equation

$$\partial F(\Theta, V)/\partial v_i = 0$$

for each v_i and substituting the resulting expression for the v's into expression 2.1 and discarding the constant terms yields

$$(2.9) \quad \tilde{F}(\Theta) = -\log_e [\sum_{fi} \{\log_e(C_{fi}(\Theta)) - \log_e(\hat{C}_{fi})\}]^2/2$$

$$-\log_e [\sum_{fi} \{M_{fi}(\Theta) - \hat{M}_{fi}\}]^2/2$$

$$-\log_e [\sum_{fi} \{\mu_{fi}^1(\Theta) - \hat{\mu}_{fi}^1\}]^2/2$$

$$-\log_e [\sum_{fi} \{\mu_{fi}^2(\Theta) - \hat{\mu}_{fi}^2\}]^2/2$$

$$-\log_e [\sum_{fi} \{\mu_{fi}^3(\Theta) - \hat{\mu}_{fi}^3\}]^2/2$$

$$-\log_e [\sum_{fi} \{\mu_{fi}^4(\Theta) - \hat{\mu}_{fi}^4\}]^2/2.$$

The advantage of the first method is that one can specify the v's exactly. This allows one to completely control their effect on the solution obtained. The disadvantage of course is that one must know what their values are.

The third method is the most elegant. One need know nothing about the v's. In fact they no longer appear in the estimation scheme at all. The disadvantage is that one has no control over the effect of the various types of data on the parameter estimates obtained.

The second method is a compromise between the other two methods with some of the advantages and disadvantages of both. It is not necessary to specify the absolute size of the variance terms v_u, but only their relative sizes. This enables one to regard the catch and effort data as the primary data with the length and weight moments providing auxiliary information by controlling the influence of the length and weight moments on the parameter estimates obtained.

We consider the second method to be preferable to the other two methods. It enables the user to examine the residuals to the model fit and to adjust the p's until they seem correct to the user. The user who finds this ad hoc approach unsettling can use the third approach. The second approach has been used in the simulations.

Determining the p's

When setting values for the p's, we have adopted the point of view that the catch and effort data $\hat{C}_{fi}$ and, $\hat{E}_{fi}$ are the main data while the weight and length moments are used to provide auxiliary information. For this reason we advocate setting the term p_0 large enough relative to p_1 through p_5 so that the fit between the $\log_e(C_{fi})$ and $\log_e(\hat{C}_{fi})$ is acceptably good. It remains to pick relative values for the terms p_1 through p_5.

It is not necessary to compute the exact variances for the sampling moments, but only to use estimates which are roughly correct. To get an idea of these variances, we have used the variances for the sampling moments for a normal distribution taken from Kendall and Stuart (1958):

Sampling moment	Variance
$\hat{M}_{fi}$	M_{fi}^2/n_{fi}
$\hat{\mu}_{fi}^1$	μ_{fi}^2/n_{fi}
$\hat{\mu}_{fi}^2$	$2(\mu_{fi}^2)^2/n_{fi}$
$\hat{\mu}_{fi}^3$	$6(\mu_{fi}^2)^3/n_{fi}$
$\hat{\mu}_{fi}^4$	$96(\mu_{fi}^2)^4/n_{fi}$

where n_{fi} is the sample size from fishery f in year i.

These variances are only exact for the sampling moments of a normal distribution, but they should reflect the approximate magnitude of the variances of these random variables relative to each other. The quantities M_{fi} and μ_{fi}^2 are not known but they can be approximated by the corresponding values of the sampling statistics $\hat{M}_{fi}^2$ and $\hat{\mu}_{fi}^2$. Thus, for example, the variance of $\hat{\mu}_{fi}^4$ can be approximated by $96(\hat{\mu}_{fi}^2)^4/n_{fi}$ and p_5 set equal to $v_0 n_{fi}/[96(\hat{\mu}_{fi}^2)^4]$.

These values for the p's should be considered to be approximations. The higher sampling moments are much more sensitive to deviations from the model's hypotheses than the observed catches. Besides, the results of the analysis lack credibility if they fit the fourth moment of the length distribution perfectly but fail to predict the observed catches. For these reasons if the observed-catch predicted-catch residuals are too large, then the value of p_0 should be increased until an acceptable agreement is obtained.

Availability and Selectivity

Two important notions in fisheries management are availability and selectivity. Availability is a concept associated with an entire age class and a fishery. It is defined to be the proportion of individuals in the age class which have a positive probability of being caught in the fishery, i.e. are vulnerable to the fishery.

Selectivity is a between age class concept. For an age class j with positive availability, the selectivity in fishery f is defined to be the probability that a vulnerable age class j fish will be caught by one unit of fishing effort in fishery f. For unavailable age classes the selectivity is defined to be 0.

If a fish is picked at random from an age class, the probability that it is caught by one unit of effort in a fishery is the product of its availability for that fishery times its selectivity for that fishery.

Availability and selectivity will be termed age dependent if they differ among age classes.

The difference between availability and selectivity becomes clear when the fishing effort is very large, for in this case essentially all vulnerable fish are caught. Consider an age class which has an availability of 0.50 and a selectivity of 0.05 versus one with an availability of 1.0 and a selectivity of 0.025. A fish picked at random from either cohort will have a probability of 0.025 of being caught by one unit of fishing effort. For very large fishing effort, however, only 50% of the former cohort will be caught while all of the latter cohort will be caught.

Most age-structured models use age-dependent selectivity while the availability for all age classes is assumed to be 1 (Doubleday 1976; Fournier and Archibald 1982; Deriso et al. 1985). In addition, in these models the selectivity is independent of the history of exploitation of the stock by the fishery.

The theory we shall develop can include both age-dependent availability and selectivity, and the age dependence of both can depend on the history of exploitation of the fishery.

Groups

Age-dependent availability and selectivity are introduced into the model by using the concept of groups first introduced by Deriso.

The general idea is to consider the members of a fish population as belonging to a set of distinct groups. The members of any group are all assumed to experience the same natural and fishing mortality in any year. New recruits are assumed to enter the first group after a lag of k years. During their lifetimes, individual fish proceed sequentially through the groups so that in any year a fish presently in group g has a probability $1 - m_g$ of proceeding on to group $g + 1$. Otherwise it remains in group g.

The movement of fish from one group to the next is assumed to take place at the end of each year. The fisheries are assumed to take place at the beginning of each year over a period of time so short that mortality from natural causes can be ignored. Mortality from natural causes operates throughout the year. (This particular form of the assumed relationship between fishing mortality and natural mortality is adopted for convenience. It could easily be modified to accommodate more complex situations.)

There are two different schemes by which the fish can move through the groups. In the first scheme, which seems to be a generalization of the methods employed by Deriso for his partial recruitment model, the fish that move from group g to group $g + 1$ at the end of a given year are considered to be group $g + 1$ fish and then have a probability $1 - m_{g+1}$ of moving to group $g + 2$ in the same year. Under this scheme it is possible for a group 1 fish to move through all the groups in one year. Under the second scheme, group g fish move to group $g + 1$ with probability $1 - m_g$ and remain in that group until the next year.

The two sets of schemes yield the same stock dynamics for the one group case and become increasingly different as the

number of groups is increased.

Since an understanding of the concept of the groups is essential for an appreciation of the general theory, some examples are presented. In these examples we shall assume that there is only one fishery and that the second scheme is employed for the movement of the fish through the groups, i.e. the fish can move at most one group in each year.

To see how the group concept can produce age-dependent availability and selectivity, it is necessary to be able to calculate the probability that a fish of age j belongs to group g. This probability will depend on the survival rates from natural mortality l_u, $1 \leq u \leq g$, the fishing survival rates s_{iu}, $1 \leq u \leq g$, and those years i after the fish recruited, and the transition probabilities m_u $1 \leq u \leq g$. Note that the probability that fish belongs to a group g is independent of l_u, s_{iu}, and m_u for $u > g$ so that it is independent of the number of groups G as long as $G > g + 1$.

Assume that there is no fishing mortality for the first two groups so that $s_{ig} = 1$ for $g = 1, 2$ and all years i.

At the beginning of a year consider a fish which recruited r years before. It is of age $r + k$ if it is still alive. If the fish is in group 1, then it has remained there for r years. For each year the probability that the fish lives and remains in group 1 is $l_1 m_1$. Thus, the probability that it remains in group 1 for r years is $l_1^r m_1^r$. (The events are assumed to be independent.)

To compute the probability that an age $r + k$ fish is in group 2, note that it can move to group 2 at the end of any one of the r years beginning with the year it recruited. Suppose it moves at the end of the qth year. That means that it experienced the event "remain in group 1" $q-1$ times and experienced the event "move to group 2" one time. Also, since it was in group 1 for q years, it experienced the event "survive in group 1" q times. Since it has spent $r-q$ years in group 2, it has experienced the event "survive in group 2" $r-q$ times and the event "remain in group 2" $r-q$ times. The collection of these events has a probability of $l_1^q m_1^{q-1} (1 - m_1) l_2^{r-q} m_2^{r-q}$ of occurring, which on summing over q yields

$$(3.1) \quad \sum_{q=1}^{r} l_1^q m_1^{q-1} (1 - m_1) l_2^{r-q} m_2^{r-q}$$

as the probability that an age $r + k$ fish lies in group 2.

If there are only two groups, then $m_2 = 1$. If we also assume that $l_1 = l_2 = 1$, expression 3.1 simplifies to

$$(3.2) \quad l^r (1 - m_1^r).$$

Expression 3.2 is the probability that a fish of age $r + k$ lies in group 2 for the 2 group model when there has not been any fishing for the last r years.

For an age $r + k$ fish which is still alive, it follows that the probability that it is in group 1 is m_1^r while the probability that it is in group 2 is $1 - m_1^r$. If group 1 fish have no probability of being caught in the fishery while group 2 fish do, then when fishing begins in the next year there is an age-dependent fishing availability curve which is equal to 0 for all age classes consisting of fish of age less than $k + 1$ and $1 - m_1^r$ for all age classes consisting of fish of age $r + k$. Since all group 2 fish have an equal probability of being caught, this model has no age-dependent selectivity.

The form of the age-dependent availability depends on the history of exploitation. To see this, assume that for the previous year the fishing has been so heavy that the second group is essentially empty. At the beginning of the year the probability that a (living) fish of age $r + k$ is in group 1 is m_1 and $1 - m_1$ that it is in group 2. Thus, in this case the availability of the fish is equal to 0 for all age classes consisting of fish of age less than $k + 1$ and equal to $1 - m_1$ for all age classes consisting of fish of age greater than k.

The removal of the age dependence in the availability curve at high exploitation rates is a consequence of the simplicity of the model. Since all fish in the first group are considered to be identical, they all have the same probability of moving to group 2 in any year, independent of what their age happens to be. If this assumption is considered to be too simplistic it is possible to remedy it by employing more complex models with more groups.

Consider a three-group model where all the groups have the same survival rate from natural mortality which is denoted simply by l and that $m_1 = m_2 = m$. We assume that only the third group is vulnerable to the fishery.

At the beginning of a year, it follows that the probability that a fish of age $r + k$ has a probability $l^r m^r$ of being alive and in group 1, while from expression 3.1 it follows that it has a probability of $r l^r m^{r-1} (1 - m)$ of being alive and in group 2.

Let

$$(3.3) \quad u = r (1 - m)/m.$$

It follows that given that a fish of age $r + k$ is alive and lies in group 1 or 2, then the probability is

$$(3.4) \quad 1/(1 + u)$$

that it lies in group 1 and

$$(3.5) \quad u/(1 + u)$$

that it lies in group 2.

Now assume that in the year in question the fishing has been very intensive so that group 3, the only group vulnerable to the fishery, has been fished out. This means that in the following year all group 3 fish must come from group 2. From expressions 3.4 and 3.5 it follows that the probability that an age $k + r + 1$ fish is alive and lies in group 1 or group 2 and is therefore not vulnerable to the fishery is

$$(3.6) \quad (1 + mu)/(1 + u)$$

while the probability that it is alive and in group 3 and vulnerable to the fishery is

$$(3.7) \quad (1 - m)u/(1 + u).$$

Using the relationship 3.3, we obtain the age-dependent availability for an age $k + r + 1$ fish:

$$(3.8) \quad (1 - m)/\{m/[(1 - m)(r - 1)] + 1\}.$$

Thus, this model will produce an age-dependent availability curve even when the exploitation rate is very high. The model "remembers" some aspects of the age structure of the fish which are not vulnerable to the fishery.

This model still has no age-dependent selectivity. If both the second and third groups are vulnerable to the fishery, but with fish in these two groups having different probabilities of being captured for a unit of fishing effort, then a model with both age-dependent availability and age-dependent selectivity is obtained.

In general, as more groups are employed the model becomes more nearly age structured. Unfortunately, the model also becomes more complicated, having more parameters which must be estimated. In a given case the answer to the question of how complicated a model to employ depends on both the quality of

the data available and the complexity of the fishery being analyzed.

To illustrate the connection between the group concept and age-structured models, suppose that $m_g = 0$, $1 \leq g \leq G - 1$, while $m_G = 1$. In this case all the fish in the first $G - 1$ groups move to the next group in each year so that these groups can be identified with age classes and the model becomes age structured. The last group consists of all the older fish.

Stock Dynamics

The movement of individual fish through the groups has been given in probabilistic terms. For entire age classes we shall assume that the number of fish is so large that the proportion of fish moving through the groups can be described in a deterministic manner. Then the stock dynamics for the two schemes of moving the fish through the groups are given by equations 4.1 through 4.4 and 5.1 through 5.4, respectively.

Scheme 1

For $g = 1$:

$$(4.1)\quad N_{ik1} = m_1 R_i$$

$$(4.2)\quad N_{ij1} = m_1 l_1 s_{i-1,1} N_{i-1,j-1,1} \qquad j > k.$$

For $g > 1$:

$$(4.3)\quad N_{ikg} = m_g ((1 - m_{g-1})/m_{g-1}) N_{ikg-1}$$

$$(4.4)\quad N_{ijg} = m_g (l_g s_{i-1,g} N_{i-1,j-1,g} + (1 - m_{g-1})/m_{g-1} \times N_{ijg-1} \qquad j > k.$$

To understand the rationale behind equation 4.3, consider the case when $g = 2$. Of the recruitment R_i the $m_1 R_i$ remains in group 1 and $(1 - m_1)R_i$ moves to group 2. Because of the dynamics, only $m_2(1 - m_1)R_i$ of this remains in group 2. Thus, $N_{ik2} = m_2(1 - m_1)R_i$. Expression 4.3 is obtained by noticing that $R_i = N_{ik1}/m_1$. The derivation of 4.4 is similar.

Scheme 2

For $g = 1$:

$$(5.1)\quad N_{ik1} = R_i$$

$$(5.2)\quad N_{ij1} = m_1 l_1 s_{i-1,1} N_{i-1,j-1,1} \qquad j > k.$$

For $g > 1$:

$$(5.3)\quad N_{i,k+g-1,g} = (1 - m_{g-1}) l_{g-1} s_{i-1,g-1} N_{i-1,k+g-2,g-1}$$

$$(5.4)\quad N_{ijg} = m_g l_g s_{i-1,g} N_{i-1,j-1,g} + (1 - m_{g-1}) l_{g-1} s_{i-1,g-1} \times N_{i-1,j-1,g-1} \qquad j > k + g - 1.$$

Relationship between Stock and Recruitment

To investigate the relationship between stock and recruitment, the three-parameter stock–recruitment relationship of Deriso (1980) and Schnute (1985) with the option of including stochastic variation or "noise" has been employed. It has the form

$$(6.1)\quad R_{i+k} = \alpha \mathrm{RB}_i / (1 + \gamma\beta[\mathrm{RB}_i/\mathrm{RB}_1 - 1])^{\frac{1}{\gamma}} e^{\epsilon_i}$$

where RB_i is the reproductive biomass in year i and the ϵ_i are independent normally distributed random variables with mean 0 and equal variances σ_R^2.

Deriso's parameterization has been modified so that the parameters are more stable. As γ tends to 0, the relationship tends to a Ricker curve:

$$(6.2)\quad R_{i+k} = \alpha \mathrm{RB}_i \exp(-\beta[\mathrm{RB}_i/\mathrm{RB}_1 - 1])\, e^{\epsilon_i}$$

while for $\gamma = 1$ the Beverton–Holt stock–recruitment relationship is obtained. For a deterministic stock–recruitment relationship, the ϵ_i are set equal to 0.

Incorporating Fishing Effort Data

For simplicity we have assumed that all fisheries occur simultaneously at the beginning of the fishing period and that the fishing period is so short that mortality from causes other than fishing can be ignored. The relationship between effective effort and the survival rate from fishing is assumed to have the form

$$(7.1)\quad s_{ig} = \exp\left(-\sum_f q_{fig} E_{fi}\right)$$

while the proportion of the fish in group g which are caught by fishery f denoted by t_{fig} is assumed to satisfy the relationship

$$(7.2)\quad t_{fig} = q_{fig} E_{fi} (1 - s_{ig}) \Big/ \sum_{f'} q_{f'ig} E_{f'i}.$$

Equations 7.1 and 7.2 are simply the Beverton–Holt catch equations for simultaneous fisheries during a period where there is no natural mortality and where the instantaneous fishing mortality rate in each fishery is assumed to be proportional to $q_{fig} E_{fi}$. These equations can easily be modified to include fisheries which occur at different times of the year.

The relationships 7.1 and 7.2 serve to determine the effective effort E_{fi}.

The number of parameters q_{fig} in expressions 7.1 and 7.2 must be reduced to obtain a useful theory. The simplest method of accomplishing this is to assume that the catchability is constant so that

$$(7.3)\quad q_{fig} = Q_{f1g}$$

where each group has its own constant catchability coefficient for each fishery independent of time.

A more complicated situation arises when the catchability depends on the biomass. There are many ways to attempt to parameterize a biomass-dependent effect in the catchability. Let $\bar{B}_g$ denote the average biomass, i.e.

$$\bar{B}_g = \frac{1}{I} \sum_i B_{ig}.$$

The simplest method is to assume the relationship

$$(7.4)\quad q_{fig} = Q_{f1g} + Q_{f2g} (B_{ig} - \bar{B}_g).$$

Expression 7.4 will produce increasing catchability with decreasing biomass if $Q_{f2g} < 0$. There are two difficulties with this parameterization, however. It is bad dimensionally because the term Q_{f2g} must contain the units of (biomass)$^{-1}$. This can lead to numerical instability in the model. For some values of Q_{f2g} it can produce negative values for the catchability. Finally, since the catchability will be needed to calculate the survival rates which are then used in the difference equations which determine the B_{ig}, it is impossible to calculate the average biomass $\bar{B}_g$ in advance. A parameterization that overcomes all these difficulties is given by

(7.5) $q_{fig} = Q_{f1g} \exp [Q_{f2g} (1 - B_{ig}/B_{1g})]$.

In expression 7.5 we have employed the dimensionless expression $1 - B_{ig}/B_{1g}$ to express the relative change in biomass from year 1. In year 1 the relationship 7.5 gives a catchability $q_{f1g} = Q_{f1g}$, while if the biomass B_{ig} tends to 0 the catchability will tend to the limiting value $Q_{f1g} \exp[Q_{f2g}]$. If the $Q_{f2g} = 0$, then the catchability is constant. If the coefficient $Q_{f2g} > 0$, then the catchability increases as the biomass decreases.

Modelling Errors in the Estimated Effort $\hat{E}_{fi}$

We shall assume that the estimated effort $\hat{E}_{fi}$ is lognormally distributed and that $\log_e(\hat{E}_{fi})$ has mean $\log_e(E_{fi})$. If it is assumed that the observed catches C_{fi} are equal to the estimated catches $\hat{C}_{fi}$, the log-likelihood function for the observations is simply expression 2.5 with the first sum

$$- p_0 \sum_i \{\log_e (C_{fi}) - \log (\hat{C}_{fi})\}^2/v_0^2$$

replaced by

$$- p_0 \sum_i \{\log_e (E_{fi}) - \log_e (\hat{E}_{fi})\}^2/v_0^2.$$

Unfortunately, in the general situation where more than one group contributes to a fishery, it is not possible to proceed so directly. In equation 7.1 the effective effort $\hat{E}_{fi}$ determines the survival rates for each group. The catches, however, do not determine the survival rates except in the case where there is only one group in the fishery. Instead the relationships 7.1 become a system of constraints which the E_{fi} must satisfy. The easiest way to overcome this problem is to assume that there are errors in both the observed catches and the estimated effort, but that the errors in the observed catches are very small compared with the errors in the estimated efforts. Then the objective function 2.5 is modified by adding a term

$$p_6 \sum_{fi} \{\log_e (E_{fi}) - \log_e (\hat{E}_{fi})\}^2/v_0^2$$

to it. The penalty weight p_0 in the term

$$p_0 \Sigma \{\log_e (C_{fi}) - \log_e (\hat{C}_{fi})\}^2/v_0^2$$

is then set large relative to p_6.

If only one group is present in the fishery, the relationship 7.1 becomes

(7.6) $s_{ig} = \exp (- q_{fig} E_{fi})$

where the subscript g takes on the value appropriate value for that fishery. Assuming that $C_{fi} = \hat{C}_{fi}$, then

(7.7) $s_{ig} = (1 - \hat{C}_{fi}/B_{ig})$.

By using the relationships 7.6 and 7.7 it is possible in this case to express the effective effort E_{fi} in terms of the observed catch $\hat{C}_{fi}$ giving

(7.8) $E_{fi} = -\log_e (1 - \hat{C}_{fi}/B_{ig})/q_{fig}$.

Calculating the M_{fi} and μ_{fi}^r

Recall that in the simple one-group model the mean weight of the fish in the catch was assumed to be equal to the mean weight of the fish in the population (i.e. the group). This assumption was made because all the fish in the group were assumed to be equally likely to be caught in the fishery. In the present multigroup case, fish in different groups have different probabilities of being present in each fishery. This leads to the moments of the weight and length distributions of the catch being mixtures of the moments of the weight and length distributions of the groups in each fishery.

Let t_{fig} denote the proportion of the fish in group g which are caught in fishery f in year i. Let Y_{fijg} be the number of age j fish from group g which are caught in fishery f in year i. Then since all fish in a group are assumed to be equally likely to be caught regardless of age:

$$Y_{fijg} = t_{fig} N_{ijg}.$$

Let w_j and τ_j denote the mean weight and mean length of an age j fish. Let z_{fijgy} be the weight of the yth age j fish from group g caught in fishery f in year i. The z_{fijgy} are random variables. Let $E\{z\}$ denote the expected value of the random variable z. Then $E\{z_{fijgy}\} = w_j$. The mean weight of the catch is a random variable whose expected value M_{fi} is given by

$$(8.1) \quad M_{fi} = \sum_g \sum_{j \geq k} \sum_{y=1}^{Y_{fijg}} E\{z_{fijgy}\} \Big/ \sum_g t_{fig} N_{i \cdot g}$$

which simplifies to

$$(8.2) \quad M_{fi} = \sum_g t_{fig} \sum_{j \geq k} w_j N_{ijg} \Big/ \sum_g t_{fig} N_{i \cdot g}.$$

The expected value for the moments of the length distribution of the catches can be calculated in a similar fashion. For the higher moments there are two extra difficulties, however. It is easier to work with the expected values of the noncentral moments of the length distribution of the catches because these depend in a simple way on the noncentral moments of the length distribution of the groups present in the fishery, while the central moments depend in a more complicated fashion on the central moments of the component groups.

In addition, the higher moments of the length distribution of the catch depend on the distribution of the lengths-at-age of the fish in each age class around their means, so that this within age class variation in length must be taken into account.

Assume that for each age the lengths of the fish are normally distributed around their mean length τ_j with variance σ_L^2 where it is assumed that the variance is independent of the age j. Let x_{fijgy} denote the length of the yth age j fish from group g caught in fishery f in year i. Then x_{fijgy} is a random variable which can be written as $x_{fijgy} = \tau_j + \epsilon_{fijgy}$ where the ϵ_{fijgy} are normally distributed random variables with mean 0 and variance σ_L^2. Let λ_{fi}^r denote the rth noncentral moment of the length distribution of the catch of fishery f in year i. The λ_{fi}^r are given by

$$(8.3) \quad \lambda_{fi}^r = \sum_g \sum_{j \geq k} \sum_{y=1}^{Y_{fijg}} E\{(\tau_j + \epsilon_{fijgy})^r\} \Big/ \sum_g t_{fig} N_{i \cdot g}.$$

For a normally distributed random variable ϵ with mean 0 and variance σ_L^2, $E\{\epsilon\} = 0$, $E\{\epsilon^2\} = \sigma_L^2$, $E\{\epsilon^3\} = 0$, and $E\{\epsilon^4\} = 3(\sigma_L^2)^2$. This gives the following formulas for the λ_{fi}^r:

$$(8.4) \quad \lambda_{fi}^1 = \sum_g t_{fig} \sum_{j \geq k} \tau_j N_{ijg} \Big/ \sum_g t_{fig} N_{i \cdot g}$$

$$(8.5) \quad \lambda_{fi}^2 = \left(\sigma_L^2 \sum_g t_{fig} N_{i \cdot g} + \sum_g t_{fig} \sum_{j \geq k} \tau_j^2 N_{ijg}\right) \div \sum_g t_{fig} N_{i \cdot g}$$

$$(8.6)\quad \lambda_{fi}^3 = \left(3\sigma_L^2 \sum_g t_{fig} \sum_{j\geq k} \tau_j N_{ijg} + \sum_g t_{fig} \sum_{j\geq k} \tau_j^3 N_{ijg}\right) \Big/ \sum_g t_{fig} N_{i\cdot g}$$

$$(8.7)\quad \lambda_{fi}^4 = \left(3(\sigma_L^2)^2 \sum_g t_{fig} N_{i\cdot g} + 6\sigma_L^2 \sum_g t_{fig} \sum_{j\geq k} \tau_j^2 N_{ijg} + \sum_g t_{fig} \sum_{j\geq k} \tau_j^4 N_{ijg}\right) \Big/ \sum_g t_{fig} N_{i\cdot g}.$$

The relationship between the central and the noncentral moments of the length distribution of the catch is given by

$$(8.8)\quad \mu_{fi}^1 = \lambda_{fi}^1$$

$$(8.9)\quad \mu_{fi}^2 = \lambda_{fi}^2 - (\lambda_{fi}^1)^2$$

$$(8.10)\quad \mu_{fi}^3 = \lambda_{fi}^3 - 3\lambda_{fi}^2 \lambda_{fi}^1 + 2(\lambda_{fi}^1)^3$$

$$(8.11)\quad \mu_{fi}^4 = \lambda_{fi}^4 - 4\lambda_{fi}^3 \lambda_{fi}^1 + 6\lambda_{fi}^2 (\lambda_{fi}^1)^2 - 3(\lambda_{fi}^1)^4.$$

To include the biomass and mean weight of the fish in the catch in the model, it is necessary to assume that there is a weight–length relationship. In fisheries literature it is often assumed that the mean weight at age j of the fish w_j satisfies the relationship

$$(9.1)\quad w_j = b\tau_j^v$$

where the exponent v is estimated by regressing the logarithm of weight on the logarithm of length. The exponent v often has a value close to 3. In the present context, only integer exponents can be considered because the procedure for deriving the difference equations only works for integral exponents. We shall therefore assume that the value of v is equal to 3. If this relationship is not sufficient, then a polynomial weight–length relationship of the form

$$w_j = b_1\tau_j + b_2\tau_j^2 + b_3\tau_j^3$$

could be considered. The model can easily be modified to deal with this assumption.

Now assuming the weight–length relationship 9.1 with $v = 3$ holds, and simply denoting b_3 by b, the biomass B_{ig} of the fish in group g is given by

$$(9.2)\quad B_{ig} = b\sum_{j\geq k} \tau_j^3 N_{ijg}.$$

Similarly, the biomass of the catch C_{fi} taken in fishery f is given by

$$(9.3)\quad C_{fi} = b\sum_g t_{fig} \sum_{j\geq k} \tau_j^3 N_{ijg}$$

while the mean weight M of the fish in the catch is given by

$$(9.4)\quad M_{fi} = \left(b\sum_g t_{fig} \sum_{j\geq k} \tau_j^3 N_{ijg}\right) \Big/ \left(\sum_g t_{fig} N_{i\cdot g}\right).$$

Notice that in the above expressions we have managed to express everything in terms of some coefficients multiplied by terms of the form

$$\sum_{j\geq k} \tau_j^r N_{ijg}$$

where r is an integer between 0 and 4.

Difference Equations

To derive the desired difference equations, it is necessary to make an assumption about the form of the mean lengths τ_j. We shall assume that they lie on a von Bertalanffy curve so that

$$(10.1)\quad \tau_j = c + (a - c)(1 - \rho^j)/(1 - \rho)$$

where $0 < \rho < 1$. (This form for parameterizing a von Bertalanffy curve is discussed in Schnute and Fournier 1980.) Then

$$(10.2)\quad \tau_j^r = \sum_{q=0}^{r} C_q^r c^q (a - c)^{r-q} \left(\frac{1 - \rho^j}{1 - \rho}\right)^{r-q}$$

where $C_q^r = r!/[q!\,(r - q)!]$ so that

$$(10.3)\quad \sum_{j\geq k} \tau_j^r N_{ijg} = \sum_{q=0}^{r} C_q^r c^q (a - c)^{r-q} \times \sum_{j\geq k} \left(\frac{1 - \rho^j}{1 - \rho}\right)^{r-q} N_{ijg}.$$

For each positive integer r, let T_{ig}^r be defined by

$$(10.4)\quad T_{ig}^r = \sum_{j\geq k} \left(\frac{1 - \rho^j}{1 - \rho}\right)^r N_{ijg}.$$

In terms of the T_{ig}^r, expression 10.3 can be rewritten as

$$(10.5)\quad \sum_{j\geq k} \tau_j^r N_{ijg} = \sum_{q=0}^{r} C_q^r c^q (a - c)^{r-q} T_{ig}^{r-q}.$$

Expression 10.1 gives the general von Bertalanffy growth curve. It is possible and may be desirable to require that the length at age 0 is 0. This is accomplished by setting c equal to 0. In this case, expression 10.5 simplifies to

$$(10.6)\quad \sum_{j\geq k} \tau_j^r N_{ijg} = a^r T_{ig}^r.$$

Since all expressions of the form

$$\sum_{j\geq k} \tau_j^r N_{ijg}$$

can be expressed in terms of the T_{ig}^r, it follows that B_{ig}, C_{fi}, M_{fi}, and the μ_{fi}^r can be as well. Therefore, it only remains to show that T_{ig}^r satisfy the desired system of difference equations.

Define A_j by

$$A_j = \left(\frac{1 - \rho^j}{1 - \rho}\right) \qquad 0 < \rho < 1.$$

Then for all positive integers r, one has

$$(11.1)\quad \rho^r A_{j-1}^r = (A_j - 1)^r.$$

Applying the binomial theorem to 11.1 yields the relationship

$$(11.2)\quad \rho^r A_{j-1}^r = \sum_{q=0}^{r} (-1)^q C_q^r A_j^{r-q}$$

or

$$(11.3)\quad A_j^r - \rho^r A_{j-1}^r = \sum_{q=1}^{r} (-1)^{q+1} C_q^r A_j^{r-q}.$$

From expression 11.3 it follows that

$$\sum_{j\geq k} (A_j^r - \rho^r r_{j-1}^r) N_{ijg} = \sum_{q=1}^{r} (-1)^{q+1} C_q^r \sum_{j\geq k} A_j^{r-q} N_{ijg}$$

or

$$(11.4)\quad T^r_{ig} = \sum_{q=1}^{r} (-1)^{q+1} C^r_q T^{r-q}_{ig} + \rho^r \sum_{j \geq k} A^r_{j-1} N_{ijg}.$$

To obtain the desired system of difference equations, it is necessary to deal with the lagged term

$$(11.5)\quad \sum_{j \geq k} A^r_{j-1} N_{ijg}.$$

Lemma 1

Assume that the population dynamics are described by equations 4.1 through 4.4. Let U_j be any set of coefficients. Then for $g = 1$:

$$(11.6)\quad \sum_{j \geq k} U_{j-1} N_{ij1} = m_1 l_1 s_{i-1,1} \sum_{j \geq k} U_j N_{i-1,j,1} + m_1 U_{k-1} R_i$$

and for $g > 1$:

$$(11.7)\quad \sum_{j \geq k} U_{j-1} N_{ijg} = m_g l_g s_{i-1,g} \sum_{j \geq k} U_j N_{i-1,jg} + m_g (1 - m_{g-1})/m_{g-1} \sum_{j \geq k} U_{j-1} N_{i,j,g-1}.$$

Applying this result to the lagged term 11.5 and substituting the result into expression 11.4 yields, for $r = 0$, theorem 1.

Theorem 1

Suppose that the populations' dynamics are described by equations 4.1 through 4.4 Then the quantities $N_{i \cdot g}$ satisfy the relationships for $g = 1$:

$$(11.8)\quad N_{i \cdot 1} = m_1 l_1 s_{i-1,} N_{i-1,1} + m_1 R_i$$

and for $g > 1$:

$$(11.9)\quad N_{i \cdot g} = m_g l_g s_{i-1,g} N_{i-1 \cdot g^{-1}} + m_g (1 - m_{g-1})/m_{g-1} N_{i \cdot g-1}.$$

For convenience let T^0_{ig} denote $N_{i \cdot g}$. For $r > 0$ the result is theorem 2.

Theorem 2

Assume that the population dynamics are determined by equations 4.1 through 4.4 Then setting $U_j = A^r_j$ and applying lemma 1 for all integers $r > 0$ and for $g = 1$ and $i > 1$:

$$(11.10)\quad T^r_{i1} = \rho^r l_1 m_1 s_{i-1,1} T^r_{i-1,1} + \sum_{q=1} (-1)^{q+1} C^r_q T^{r-q}_{i1} + \rho^r m_1 A^r_{k-1} R_i$$

and for $g > 1$ and $i > 1$:

$$(11.11)\quad T^r_{ig} = \rho^r l_g m_g s_{i-1,g} T^r_{i-1,g} + \sum_{q=1}^{r} (-1)^{q+1} \times C^r_q T^{r-q}_{ig} + m_g (1 - m_{g-1})/m_{g-1} \times \sum_{q=0}^{r} (-1)^q C^r_q T^{r-q}_{ig-1}.$$

The corresponding result for the scheme of moving through the groups given by equations 5.1 through 5.4 is lemma 2.

Lemma 2

Assume that the population dynamics are described by equations 5.1 through 5.4. Let U_j be any set of coefficients. Then for $g = 1$:

$$(11.12)\quad \sum_{j \geq k} U_{j-1} N_{ij1} = m_1 l_1 s_{i-1,1} \sum_{j \geq k} U_j N_{i-1,j1} + U_{k-1} R_i$$

and for $g > 1$:

$$(11.13)\quad \sum_{j \geq k+g-1} U_{j-1} N_{ijg} = m_g l_g s_{i-1,g} \times \sum_{j \geq k+g-1} U_j N_{i-1,jg} + (1 - m_{g-1}) l_{g-1} s_{i-1,g-1} \times \sum_{j \geq k+g-2} U_j N_{i-1,j,g-1}.$$

Theorem 3

Suppose that the population dynamics satisfy equations 5.1 through 5.4. Then the $N_{i \cdot g}$ satisfy the relationships for $g = 1$ and $i > 1$:

$$(11.14)\quad N_{i \cdot 1} = m_1 l_1 s_{i-1,1} N_{i-1 \cdot 1} + R_i$$

and for $g > 1$ and $i > 1$:

$$(11.15)\quad N_{i \cdot g} = m_g l_g s_{i-1,g} N_{i-1 \cdot g} + (1 - m_{g-1}) l_g s_{i-1,g-1} N_{i-1 \cdot g-1}.$$

For r > 0, the result is theorem 4.

Theorem 4

Assume that the populations dynamics are determined by equations 5.1 through 5.4. Then setting $U_j = A^r_j$ and applying lemma 2 yields for all integers $r > 0$ and for $g = 1$ and $i > 1$:

$$(11.16)\quad T^r_{i1} = \rho^r l_1 m_1 s_{i-1,1} T^r_{i-1,1} + \sum_{q=1}^{r} (-1)^{q+1} C^r_q T^{r-q}_{i1} + \rho^r A^r_{k-1} R_i$$

and for $g > 1$ and $i > 1$:

$$(11.17)\quad T^r_{ig} = \rho^r l_g m_g s_{i-1,g} T^r_{i-1,g} + \sum_{q=1}^{r} (-1)^{q+1} C^r_q T^{r-9}_{ig} + \rho^r (1 - m_{g-1}) l_{g-1} s_{i-1,g-1} T^r_{i-1,g-1}.$$

This completes the derivation of the desired systems of difference equations.

Calculating the Model Parameters

These results can be used to calculate the values of the model parameters as follows.

Step 1

Pick values for all free parameters, free parameters being those parameters which are not calculated in terms of other parameters. Whether a parameter is free or not may depend on the particular form of the model hypotheses. For example, if the form of the model where it is assumed that there is no error in the estimated efforts $\hat{E}_{fi}$ is used, then the E_{fi} are set equal to the $\hat{E}_{fi}$ so they are not free parameters. In general, the free parameters may include Q_{f1g}, Q_{f2g}, E_{fi}, T^r_{1g}, a, b, ρ, α, β, λ, a, l_g, and σ^2_L.

Any of these parameters may be given a fixed value if their true value is assumed to be known. For example, b could be determined by performing a regression of the logarithm of the fish weights on the logarithm of the fish lengths. The variance term σ^2_L could be estimated by aging fish, inference from tag recovery, or by examination of length frequency data. If a

group is not considered available to the fishery, then the coefficients Q_{f1g} and Q_{f2g} would be set equal to 0 for that group and fishery. Let $i = 1$.

Step 2

Calculate the biomasses B_{ig} from equations 10.6 and 9.2.

Step 3

Calculate the catchabilities q_{fig} from equation 7.5.

Step 4

Calculate the survival rates s_{ig} from equation 7.1.

Step 5

Calculate the proportions caught t_{fig} from equation 7.2.

Step 6

Calculate the catches C_{fi} from equations 10.6 and 9.3.

Step 7

Calculate the mean weights of the catches M_{fi} from equations 10.6 and 9.4.

Step 8

Calculate the noncentral moments of length distribution λ^r_{fi} of the catches from equations 10.6 and 8.4 through 8.7.

Step 9

Calculate the central moments of the length distribution μ^r_{fi} of the catches from equations 8.8 through 8.11.

Step 10

Calculate the reproductive biomass RB_i. This calculation depends on the particular model assumptions. For example, in the two-group case used in the simulations, group 1 fish were assumed to be sexually immature and RB_i was set equal to B_{i2}, the biomass of the sexually mature group 2 fish.

Step 11

Calculate R_{i+1} from the stock–recruitment relationship, equation 6.1. For $2 \leq i + 1 \leq k$ the reproductive biomass for the recruitment R_{i+1} is not known. We have used RB_1 in equation 6.1 for $2 \leq i + 1 \leq k$.

Step 12

Calculate the $T^r_{i+1,g}$ by using equations 11.8 through 11.11 if the population dynamics are given by equations 4.1 through 4.4 and by using equations 11.14 through 11.17 if the population dynamics are determined by equations 5.1 through 5.4.

Step 13

Set $i = i + 1$. If $i \leq I$ (the number of years of fishing data), then go to step 2; otherwise, stop.

Simulations

When choosing the hypotheses used for the simulations, several objectives were considered. We wanted to simulate data which had enough stochastic irregularity to represent a real fishery. Also, we wanted to be able to relate our results to the previous work of Ludwig and Walters. To this end our generalization of Deriso's partial recruitment model was used in the simulations. To make the simulations realistic, considerable stochastic error was included in both the stock–recruitment relationship and the relationship between estimated effort and effective effort. Finally, a relatively short time period of 20 yr (Ludwig and Walters used 50 yr) of fishing data were employed.

The simple von Bertalanffy growth curve with a length of 0 at age 0 was used.

The model has two groups of fish. The first group is assumed to be completely unavailable to the fishery, and the catchability for fish in this group is fixed at 0. The second group consists of the fishable stock.

The parameters determining the population dynamics of the stock (Table 1) have been chosen so that the stock consists of slow-growing fish with low productivity. The catchability has been given a large biomass-dependent component which leads to approximately a 90% increase in catchability when the stock has been fished to 50% of its initial biomass. The stochastic noise in the relationship between the observed effort and the effective effort was assumed to be multiplicative lognormal with a variance of 0.09.

A Ricker stock–recruitment relationship was employed with a multiplicative lognormal random variation with variance 0.09. The form of estimation with the stochastic error in the effort – fishing mortality relationship was employed.

The particular combination of growth, mortality, and stock–recruitment parameters produces a virgin biomass at a level which is 1.5 times the biomass which produces the maximum recruitment. The reproductive biomass RB_i was set equal to the biomass of the fishable stock B_{i2}.

To produce length data which could not be used for age estimation through the use of an age–length relationship or by length frequency analysis using a method such as that described in Schnute and Fournier (1980), the variance of the distribution of the lengths-at-age of the fish was chosen so that the length distributions of neighboring age classes have a large overlap. The mean lengths of age 3 and age 4 fish are 5.1 and 6.4 so that the mean length increment is 1.3. The variance σ^2_L was set equal to 1.0:

	Mean length											
Age	1	2	3	4	5	6	7	8	9	10	11	12
Mean length	2.0	3.7	5.1	6.4	7.4	8.3	9.1	9.7	10.2	10.7	11.1	11.4
Length change	1.7	1.4	1.3	1.0	0.9	0.8	0.6	0.5	0.5	0.4	0.3	

so that the difference between the mean lengths divided by the sum of the standard deviations for the first two age classes in the fishery is equal to 0.65. Hasselblad (1966) demonstrated that for mixtures of normal distributions there is almost no information about the means or proportions of the components of the mixture when the difference between the means divided by the sum of the standard deviations is less than 1.0. In the present situation the separation is much less than that, so that no analysis of the length frequency data by itself could be expected to produce accurate estimates of the age structure of the catch.

The catch samples were simulated by generating random samples of 500 fish from the catch.

Table 2 gives catch data for one realization of the simulations. All the data here have their true values. Thus, for example, the effort shown is the true effective effort. The estimated effort used in the estimations process had a 30% random error imposed on it. Of course the manager does not know the biomass of the fishable populations or the survival rates. They are included here for comparison. Because of the effect of density-dependent catchability, the catch per unit effort (CPUE) is still about 51% of its initial value, while the

TABLE 1. Parameters values for example 1.

		Remarks
l	= 0.90	l has the same value for both groups
ρ	= 0.85	Slow growing. Requires about 14 yr to reach 90% of maximum length
a	= 2.0	Mean length at age 1
b	= 2.5	Parameter determining length–weight relationship
Q_{112}	= 0.0018	Gives a fishing mortality rate of 0.11 for the first year
Q_{122}	= 1.3	Produces a strong density-dependent component to the catchability
m_1	= 0.50	Annual rate of entry to the fishable stock
V_6	0.30	Standard deviations in the effort – fishing mortality relationship
α	= 0.36×10^{-4}	Coefficients of the Ricker stock–recruitment relationship
β	= 1.5	
σ_R^2	0.30	Standard deviation in the stock–recruitment relationship
σ_L^2	= 1.0	Standard deviations of the distribution of the lengths of the fish around their mean
Age at recruitment to group 1	3	

biomass of the fishable population has actually decreased to about 20% of its initial value.

Over the 20-yr period the mean weight of the fish in the catch has decreased from 31 to 18. This observation might cause the manager some concern, but with a model that uses only catch and effort data there is no way to incorporate the mean weight data into the analysis.

The Bayesian prior distributions (Table 3) were chosen to somewhat overestimate the ability of the stock to withstand exploitation in that the growth rate is higher than the true growth rate and the natural survival rate is underestimated, while the degree of biomass dependence is underestimated by over 50%. The reason for picking these values for the Bayesian prior distributions is that we are interested in determining whether the model is capable of detecting the fact that the stock is much more vulnerable to fishing than the parameter values favored by the Bayesian assumptions would indicate.

Note that it was necessary to impose an upper limit on the mean length of the fish in group 1. Otherwise the model tended to allow the fish to remain in group 1 for too long a period so that the mean lengths of group 1 and group 2 fish became almost the same. In the simulations, the actual mean length of fish in group 1 was never greater than 6.4, so that the assumption that the manager knows that it should be less than 7.0 is not unreasonable.

Choosing an Optimal Policy

Many criteria could be used to define an optimal policy. The criterion chosen was to attempt to maximize long-term average yield by choosing the optimal level of fishing effort. To determine the long-term average yield the simulator was run using the true parameter values for 60 yr at a fixed level of effort and the average yield for the years 50–60 calculated. This process was repeated 100 times so that the distribution of the average yields and the average biomass between years 50 and 60 could be determined. This Monte Carlo approach can be easily adapted to investigate other policies. The true expected mean yields at each effort level together with their coefficient of variation and the corresponding mean biomass levels are as follows:

Effort	0	10	15	20	25	30	35	40	45	50
Catch	0.0	100	140	180	200	200	170	140	90	60
Coeff. of var.	0.00	0.02	0.03	0.06	0.09	0.11	0.15	0.16	0.17	0.18
Biomass	5600	4600	4000	3300	2500	1800	1107	701	308	201

The maximum expected average yield is at an effort of 25. The coefficient of variation of the catch shows an increasing trend which is caused by the decrease in stability of the population as the harvesting rate is increased.

This procedure allows one to estimate the optimal level of effort provided that the correct values of the parameters are known. For investigating the performance of the model the values of the parameters are not known but must be estimated by analyzing simulated data. The procedure used is the following.

The simulator is run with the true parameter values to produce 20 yr of simulated fisheries data. These simulated data are then analyzed by the model and estimates of the parameters obtained. These parameter estimates are then used in the simulator with the 60-yr fishery to estimate long-term yields at various effort levels. The simulations were repeated 25 times at each effort level so that an estimate of the expected mean yield together with an estimate of the standard deviation in expected mean yield was produced. The rule used to pick the optimal level of effort was to choose the minimum effort level for which the estimated expected mean yield was within one standard deviation of the maximum expected mean yield. This produces a slightly conservative policy compared with just picking the effort level for which the estimated expected mean yield is the largest, and also penalizes the expected mean yield slightly if it has a large estimated variance.

This entire set of analyses and simulations was repeated 50 times to investigate how well the method was able to detect the biomass-dependent component of catchability and how well it was able to estimate the optimal effort level:

Effort level	10	15	20	25	30	35	40	45	50	55
Number of times picked	3	3	12	12	12	5	0	1	0	2

The mean of the estimates for Q_{122} was 1.17, while their standard deviation was 0.42.

To insure that the apparent ability of the model to detect biomass-dependent catchability was not just an artifact of the estimation process, the simulations were carried out again with the effort corrected so that the biomass-dependent effect was removed. The resulting estimates for Q_{122} had a mean of 0.34 and a standard deviation of 0.38.

Determining the Age at Recruitment

The true age at recruitment of 3 may not be known. The sensitivity of the model to changes in this parameter were investigated by using estimated ages of recruitment of 2 and 4 and redoing the 50 sets of simulations. For assumed age of recruitment of 2:

TABLE 2. Annual statistics for the simulated catch.

Year	Biomass	Catch (weight)	Effort	Mean weight	Mean length	Survival rate	CPUE
1	5606	573	60	31	10.2	0.898	9.5
2	5043	583	60	30	10.2	0.884	9.7
3	4487	586	60	30	10.1	0.869	9.8
4	3947	579	60	29	10.0	0.853	9.6
5	3437	562	60	28	9.8	0.836	9.4
6	2968	535	60	26	9.6	0.819	8.9
7	2549	502	60	25	9.3	0.803	8.3
8	2186	464	60	23	9.1	0.788	7.7
9	1878	153	20	21	8.9	0.918	7.6
10	1900	154	20	21	8.8	0.919	7.7
11	1934	156	20	20	8.8	0.919	7.8
12	1972	158	20	21	8.9	0.920	7.9
13	2007	159	20	21	8.9	0.920	8.0
14	2040	161	20	21	9.0	0.921	8.1
15	2069	162	20	21	9.0	0.922	8.1
16	2096	453	60	21	9.0	0.784	7.5
17	1818	416	60	21	8.9	0.771	6.9
18	1571	378	60	20	8.8	0.759	6.3
19	1360	341	60	19	8.6	0.749	5.6
20	1184	307	60	18	8.5	0.740	5.1

TABLE 3. Bayesian prior distributions.

Parameter	Mean	SD	Remarks
ρ	0.80	0.1	Normal distribution
l	0.80	0.1	Normal distribution
m_1	0.40	0.1	Normal distribution
Mean length at recruitment	5.0	0.7	Normal distribution true value = 5.2
Q_{112}	0.0036	0.7	Multiplicative lognormal distribution
Q_{122}	0.75	0.7	Normal distribution
Mean length of fish in group 1	<7.0		Necessary to stabilize the estimation procedure

Effort level	10	15	20	25	30	35	40	45	50	55
Number of times picked	5	1	10	12	5	5	3	5	2	0

The results are degraded considerably by underestimating the age of recruitment. If no other data are available, a natural way of determining which value to use for the age at recruitment is to pick the one for which the mode of the posterior distribution achieves its higher value. Using this criterion, the correct value of the age of recruitment of 3 would have been picked over that of 2 in 46 of 48 cases considered (two runs aborted with numerical errors).

The estimates for an age of recruitment of 4 are as follows:

Effort level	10	15	20	25	30	35	40	45	50	55
Number of times picked	2	3	11	15	9	4	4	0	0	2

The estimates are evidently not so sensitive to overestimation of the age of recruitment as they are to its underestimation. This is fortunate because the model was not as capable of distinguishing between the age of recruitment estimates of 3 and 4 as it was between 2 and 3. The correct value of the age of recruitment of 3 would have been picked over that of 4 in 37 of the 50 cases.

Conclusions

The results of the simulations illustrate that through the use of the total catch, the mean weight of the catch, and effort and length data, it is possible to estimate optimal harvesting rates in cases where catchability is not constant so that there is no simple index of abundance provided by CPUE data, provided that the fishery is managed in such a way as to provide sufficient contrast in the data.

To a person accustomed to certainty and precision, the number of times that the method picked a suboptimal policy might appear disconcerting. It is, however, a fact that in fisheries management one must deal with noisy (i.e. to some extent unpredictable) systems which themselves must be analyzed with data of varying accuracy. The purpose of mathematical modelling in fisheries management is to provide the best analysis possible in a given circumstance.

It should also be remembered that for a real fishery the analysis would be ongoing. For the scenarios where the estimated optimal level of fishing is too high the model would obtain valuable information from subsequent years of fisheries data as the stock declined further. Eventually it would be realized that the optimal level of effort is less than it had previously been estimated to be.

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References

CLARK, C. W., AND M. MANGEL. 1979. Aggregation and fishery dynamics: a theoretical study of schooling and the purse seine tuna fisheries. Fish. Bull. 77 (2): 317–337.

DERISO, R. B. 1980. Harvesting strategies and parameter estimation for an age structured model. Can. J. Fish. Aquat. Sci. 37: 268–282.

DERISO, R. B., T. J. QUINN II, AND P. R. NEAL. 1985. Catch age analysis with auxiliary information. Can. J. Fish. Aquat. Sci. 42: 815–824.

DOUBLEDAY, W. G. 1976. A least square approach to analyzing catch at age data. Int. Comm. Northwest Atl. Fish Res. Bull. 12: 69–91.

FOURNIER, D., AND C. ARCHIBALD. 1982. A general theory for analyzing catch at age data. Can. J. Fish. Aquat. Sci. 39: 1195–1207.

HASSELBLAD, V. 1966. Estimation of parameters for a mixture of normal distributions. Technometrics 8: 431–444.

KENDALL, M. G., AND A. STUART. 1958. The advanced theory of statistics. 3rd ed. Hafner Publishing Company, New York, NY. 243 p.

LUDWIG, D., AND R. HILBORN. 1983. Adaptive probing strategies for age-structured fish stocks. Can. J. Fish. Aquat. Sci. 40: 559–565.

LUDWIG, D., AND C. J. WALTERS. 1985. Are age-structured models appropriate for catch-effort data? Can. J. Fish. Aquat. Sci. 42: 1066–1072.

PELLA, J. J. AND P. K. TOMLINSON. 1969. A generalized stock production model. Inter-Am. Trop. Tuna Comm. Bull. 13: 421–496.

SCHAEFER, M. B. 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Inter-Am. Trop. Tuna Comm. Bull. 2: 245–285.

SCHNUTE, J. 1977. Improved estimates from the Schaefer production model: theoretical considerations. J. Fish. Res. Board Can. 34: 583–603.

1985. A general theory for analysis of catch and effort data. Can. J. Fish. Aquat. Sci. 42: 414–429.

SCHNUTE, J., AND D. FOURNIER. 1980. A new approach to length frequency analysis: growth structure. Can. J. Fish. Aquat. Sci. 37: 1337–1351.

Wind-Forced Hydrodynamics and Their Interaction with Larval Fish and Plankton Abundance: A Time-Series Analysis of Physical–Biological Data[1]

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Taggart, C. T., and W. C. Leggett. 1987. Wind-forced hydrodynamics and their interaction with larval fish and plankton abundance: a time-series analysis of physical–biological data. Can. J. Fish. Aquat. Sci. 44: 438–451.

We evaluated methods to measure simultaneously biological and physical properties essential for estimating short-term mortality of larval fish. We used the data to test Templeman's watermass exchange hypothesis and the associated safe-site hypothesis. Synoptic estimates of larval capelin (*Mallotus villosus*) and microzooplankton particle density were obtained simultaneously with a scale resolution of 200 m (horizontal), 2–4 m (vertical) and 6–8 h (temporal) in a 1-km^2 coastal embayment in eastern Newfoundland. Statistically significant population estimates were derived from multiple regression models incorporating a limited number of samples. Spectral analysis of wind and current time-series and analysis of large-scale temperature oscillations were consistent with Templeman's hypothesis. Nearshore current responded to cross-shore wind forcing at periods of 2–6 d. Larval capelin abundance oscillations were coherent with wind and with current at periods of ~5 d, consistent with the watermass exchange and safe-site hypotheses. Although larvae and microzooplankton abundances showed similar spectral density and were in phase, their coherence was weak. Integrated measures of onshore wind and of the onshore–offshore wind spectrum were correlated, and either can be used as a composite measure of the considerable interannual variation evident in the frequency, magnitude, and duration of onshore winds, and hence of watermass exchange.

Afin de déterminer la mortalité à court terme des larves de poisson, les auteurs ont évalué des méthodes de quantification simultanée des propriétés biologiques et physiques. Les données ont été utilisées pour vérifier l'hypothèse de Templeman relative à l'échange de la masse d'eau et l'hypothèse connexe sur l'existence d'un endroit sécuritaire. Dans le cas des larves de capelan (*Mallotus villosus*) et de la densité particulaire du microzooplancton, ils ont obtenu simultanément des estimations synoptiques avec une résolution à l'échelle de 200 m (horizontal), de 2–4 m (vertical) et de 6–8 h (temporel) dans une baie d'une superficie de 1 km^2 située sur le littoral est de Terre-Neuve. Des estimations de population statistiquement significatives ont été tirées de modèles de régression multiple regroupant un nombre limité d'échantillons. Une analyse spectrale des séries chronologiques de données sur le vent et les courants et l'analyse des oscillations de la température à grande échelle s'accordaient avec l'hypothèse de Templeman. Les courants littoraux ont réagi aux vents de travers qui augmentaient d'intensité par périodes de 2 à 6 j. Les oscillations de l'abondance des larves de capelan correspondaient aux vents et aux courants par périodes de ~5 j et aux hypothèses relatives à l'échange de la masse aqueuse et à l'endroit sécuritaire. L'abondance des larves et du microzooplancton montrait une densité spectrale semblable et ceux-ci étaient en phase, mais leur cohérence était faible. Des quantifications intégrées du vent du large et du spectre du vent du large et du vent de terre étaient en corrélation; les deux mesures peuvent donc être utilisées comme mesure composée de l'importante variation interannuelle évidente dans la fréquence, la force et la durée des vents du large et donc de l'échange de la masse aqueuse.

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Numerous attempts to measure larval fish mortality during early drift suggest that mortality can exceed 80% in 30 d or less (e.g. Blaxter 1974; Dahlberg 1979; Henderson et al. 1984; Ware and Lambert 1985; Fortier and Leggett 1985; Hewitt et al. 1985). However, there is no direct field evidence demonstrating that early larval mortality is related to recruitment failure, although there are numerous related hypotheses (Hjort 1914; Cushing 1972, 1975; Lasker 1975; Tilseth and Ellertsen 1984; Pearcy 1962; Nelson et al. 1977; Bailey 1981; Frank and Leggett 1982b; Leggett et al. 1984; Sinclair et al. 1985). It is no secret that this lacuna stems mainly from the appreciable logistic problems inherent in quantitative sampling of larval fish populations and the use of inadequate space–time sampling scales (Smith 1978, 1981; Sharp 1980). Furthermore, there is little evidence regarding the relative impact of physical variables on realized mortality and on the mortality observed, which is potentially biased by the constraints of the existing techniques.

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These problems not withstanding, there remains an important need to develop the sampling protocols and analytical techniques required to study and confidently estimate larval mortality directly in the field. Twenty years ago, Gulland (1965) recognized the importance of a thorough egg and larval survey designed to measure mortality directly and recommended that sampling must be frequent and concentrated in a small and well-defined area if meaningful results are to be obtained. The need to evaluate biological phenomena in light of the relevant physical variables, and to do so within appropriate time and space scales, has been repeatedly stated (Sharp 1980; Rothlisberg 1982; Norcross and Shaw 1984; Frank and Leggett 1982b; Fortier and Leggett 1984). A more general call for the use of this interdisciplinary approach has been voiced by Legendre and Demers (1984).

Fulfilling these requirements renders more difficult the already demanding task of measuring changes in abundance of larvae in space and time while at the same time continuously accounting for immigration and emigration, both of which are essential to develop precise measures of the dynamics of any population. Fortunately, during early larval drift, the horizontal movements of larvae are largely passive (Fortier and Leggett 1982). However, active vertical migration can make estimates of dispersal distances and directions, and therefore estimates of immigration, emigration, and mortality, highly dependent on the speed and direction of currents in space and with time (Rothlisberg 1982; Fortier and Leggett 1983). Several points should be seriously considered *prior* to examining mortality relationships (Smith 1981):

(1) Different sampling strategies are required to test different hypotheses; space-extensive surveys for hypotheses concerned with transport and time-intensive surveys for those concerned with the critical period or food availability.

(2) If hypotheses directly related to food limitation are to be evaluated, sampling must be conducted with the spatial and temporal intensity sufficient to also sample the food of the larvae with high definition.

(3) The paucity of tests of the various hypotheses to date has been caused by failure to identify the spatial and temporal sampling intensity required to address any single hypothesis.

We conclude the following:

(1) Research must concentrate *first* on developing methods that allow for precise short-term mortality estimates, and only then on examining how mortality may relate to various biotic/abiotic influences.

(2) The methods employed will require sampling to be conducted at scales which approach those relevant to fish larvae, and at the scale of variation inherent to their physical environment.

(3) Initially, it is necessary to develop and evaluate these methods in well-defined areas where the variation in the larval population size (including the effects of immigration and emigration) and variation in the physical environment can be assessed synoptically and with confidence (John 1984).

(4) It is also necessary to begin with a temporally intensive sampling programme over a small area near the maximum concentration of larvae (Smith 1981).

Some success with this approach has been achieved by Frank and Leggett (1981a, 1981b; 1982a, 1982b; 1983a, 1983b) in their studies on the causes and magnitude of egg and preemergent larval mortality in beach-spawning capelin (*Mallotus villosus*) and the relationship between the sources of mortality and year-class variation in the species (Leggett et al. 1984). We adopted a similar approach in this study.

Our overall objective was to develop precise estimates of short-term larval mortality in capelin during early drift and to evaluate the relationship between this mortality and food availability and larval abundance. In this paper we detail and evaluate sampling and analytical techniques employed to simultaneously measure biological and physical properties and sampling bias. These measurements are essential to the eventual determination of mortality estimates (in prep.).

The data developed are of the time-series form and therefore have the additional attribute of being ideally suited to a critical test of Templeman's (1966) wind-driven coastal watermass exchange hypothesis. Templeman proposed that intraseasonal variations in nearshore cod abundance in coastal Newfoundland could be explained by intermittent oscillations of warm and cold watermasses in the nearshore zones. He further hypothesized that this phenomenon was wind-driven, implying that coastal regions directionally opposite each other with respect to the prevailing winds would experience reciprocal oscillations of the two watermass types. This hypothesis was invoked by Frank and Leggett (1982b) to account for associated time-dependent variations in the abundance of emergent larval fishes and their planktonic prey and predators. This hypothesis is also fundamental to a capelin recruitment model (Leggett et al. 1984), which has been used as the basis for predictions of inshore whale abundance (Whitehead and Carscadden 1985).

Methods and Materials

Study Site

The study was conducted in Bryants Cove (47°40.5′N, 53°11.0′W), Conception Bay, Newfoundland. The cove is approximately 1 km long and 1 km wide at its mouth at which point depth exceeds 20 m (Fig. 1). Cove volume was estimated to be 5.54×10^6 m^3. Capelin spawn on a fine-gravel beach located at the head of the cove. Eggs incubate in the sediments, and hatched larvae are eventually dispersed into the water column during the occurrence of onshore winds (Frank and Leggett 1981a, 1981b).

Physical Oceanographic Data

Current speed and direction, temperature, and salinity were measured in 1982 and 1983 using five Aanderaa RCM4 current meters moored at three stations (Stations 1–3, Fig. 1). In 1983 an additional current meter was moored 4 km northeast of the cove (Station 4). Data were collected at 10-min intervals from late June to early August of each year. Depth and data record lengths for each current meter are presented in Table 1. Current direction data were decomposed into U (offshore, positive northeast) and V (longshore, positive northwest) vectors resolved around 54°, corresponding to the offshore orientation of the cove axis (Fig. 1).

Current meter data were decimated (sensu Koopmans 1974) to hourly values using an A6-A6-A7 filter (Godin 1972). This produced a "smoothed" signal free of high-frequency variations (periods <1 h). The data were further treated with an A24-A24-A25 filter to produce hourly "lowpassed" data to suppress semidiurnal and diurnal tide variations (Godin 1972) and to provide more representative values for comparison with the biological data (see below). Tidal analysis of the data (Forman 1978) revealed the residual circulation to be dominant

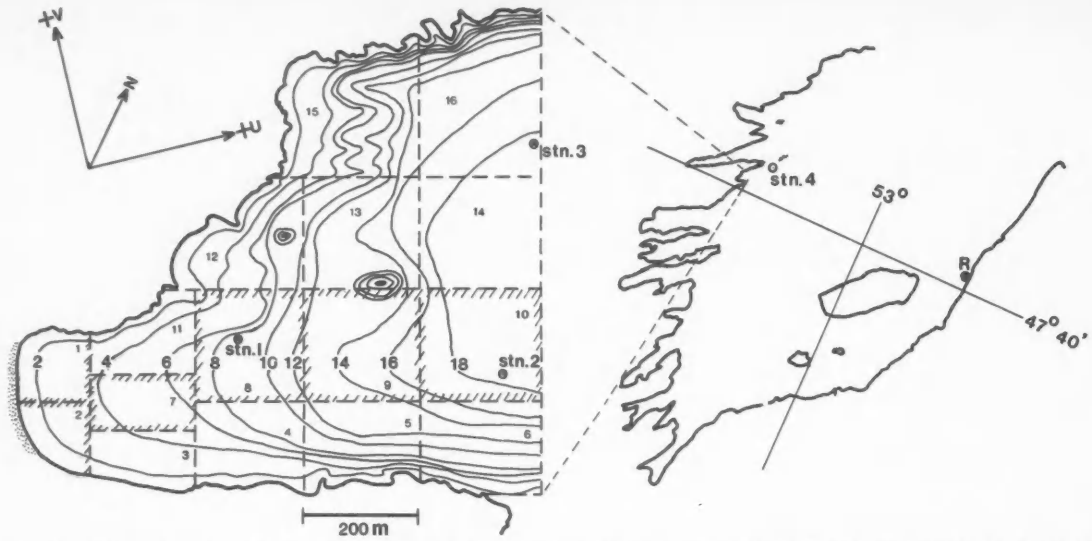

FIG. 1. Map of Conception Bay, Nfld., and bathymetric map of Bryants Cove detailing depth (m) and the dimensions and positions of the 16 grid sampling stations (1–16), the transect stations (hatched), positions of the current meter moorings (Stations 1–4), and the location of the Ryan thermograph recorder at Portugal Cove (R). The location of the capelin spawning beach is marked with stippling. Directions of U and V decomposition of wind and current are shown.

TABLE 1. Bottom and mooring depths, current speed, and length of data series for Aanderra recording current meters in Bryants Cove, Nfld.

	Year	Recording period	Depth (m)	Bottom depth (m)	Average current (cm/s)
Station 1					
Shallow	1982	10 June– 6 Aug.	4.5	9.3	6.4
	1983	13 June– 3 Aug.	4.5		6.0
Station 2					
Shallow	1982	10 June– 6 Aug.	5.9	18.3	5.5
	1983	20 June– 3 Aug.	6.4		5.3
Deep	1982	10 June– 6 Aug.	14.5		4.4
	1983	20 June– 3 Aug.	15.0		4.0
Station 3					
Shallow	1982	10 June– 6 Aug.	9.2	20.0	6.2
	1983	25 June–13 Aug.	5.8		5.4
Deep	1982	10 June– 6 Aug.	17.0		3.7
	1983	25 June–13 Aug.	15.0		3.9
Station 4					
Shallow	1983	20 June–10 Aug.	7.0	57.0	11.3

and the current at tidal frequencies to be weak. Hourly wind speed and direction data (Environment Canada, Atmospheric Environment Service, monthly meteorological summaries) were obtained for St. John's airport, located 19 km east of the centre of Conception Bay. Upwind directions in 22.5° increments were rotated 180° to downwind (oceanographic convention) and were then decomposed into U and V vectors also resolved around 54°. The hourly wind data were smoothed with a single pass of a symmetrically weighted moving average, with weightings based on the A6-A6-A7 Godin filter. Lowpassed wind signals were produced by treating the smoothed series with a symmetrically weighted moving average based on the A24-A24-A25 Godin filter. Wind stress (t_x and t_y) was calculated for the U and V-components, respectively, using the formula of Smith and Banke (1975). Wind stress was used in most of our analyses of wind data, as it reflects the energy transferred to surface waters.

Ryan temperature records taken at the bottom (10 m) on the east side of Conception Bay (Fig. 1), directly opposite Bryants Cove, were obtained from D. Keats (Memorial University of Newfoundland, St. Johns's, Nfld).

Biological Data and Development

In 1981–83, plankton samples were pumped at geographically defined stations within the cove using the system developed and evaluated in Taggart and Leggett (1984). An 80-μm plankton net was employed to collect samples at the pump discharge. In 1983, samples were collected at least daily during daylight between 25 June and 9 August (with the exception of 26 June and 5, 7, and 31 July). Sampling frequency was increased to once every 6–8 h with the occurrence of onshore winds when larval emergence was pronounced. A total of 68 sampling "sessions" were conducted over a period of 46 d. During each session we systematically sampled 1–2 m^3 (0.6–0.8 m^3/min) from each of three depth strata (0–2, 2–5, and 5–9 m, where permitted by bathymetry) either on a grid of 16 stations (a total of 31 station-strata samples) covering the entire cove or on a "transect" of 6 stations (13 station-strata samples) along the main axis of the cove and perpendicular to the spawning beach (Fig. 1). Preliminary sampling conducted in 1981 demonstrated that larval density estimates from the transect provided accurate estimates of density over the entire grid (r^2 = 0.98, n = 33). Grid stations were spaced on approximate 200-m centres, each grid covering 4 × 10^4 m^2.

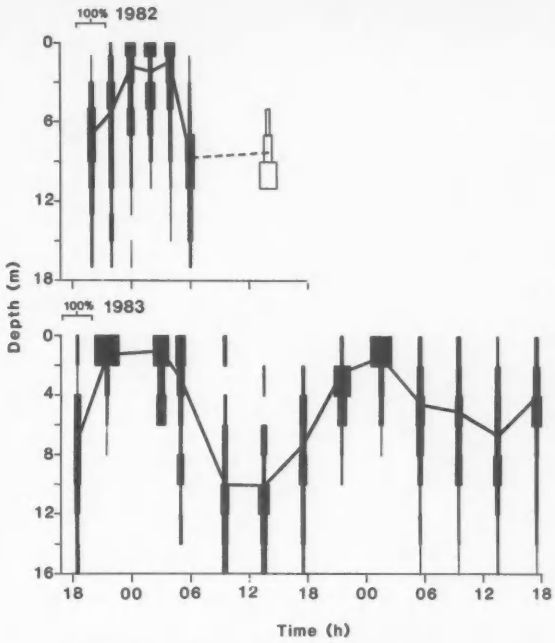

FIG. 2. Proportional diel depth distribution of capelin larvae sampled in Bryants Cove on 9–10 August 1982 and 26–28 July 1983. The solid line joins the statistical centre-of-mass of each distribution. No samples were collected below 11 m during the last sample period of 1982.

Samples were horizontally and vertically integrated by moving the sampling intake within the confines of the station while at the same time undulating the intake within the specified depth stratum. Grid boundaries were determined during daylight by noting the boat position relative to specific shore markers and at night relative to narrow-beam marker lights installed around the cove. The 16-station grid was sampled within 2 h and the 6-station transect within 1 h.

All samples were preserved immediately in 4% formalin–seawater buffered with sodium borate. Samples were subsequently completely sorted for capelin larvae and the remaining biota were then filtered through a 750-μm sieve. The fraction <750 μm was subsampled and its particle size composition was determined with a TA-II Coulter Counter fitted with a 2000-μm-aperture tube. The sampling tube was calibrated with uniform spherical particles with diameters of 91, 109, 175, 278, 350, and 472 μm. Prior to counting, each subsample was rinsed over a 40-μm mesh, drained, and completely mixed into 1000 ml of a 75% (by volume) glycerol– distilled water (5% NaCl by weight) electrolyte. Contamination of the electrolyte by bubbles which formed on the external electrode was avoided by enclosing the electrode in a glass tube open at either end, with the upper end extending above the surface of the electrolyte. Background counts of the electrolyte were maintained below 2% of the average total particle count. Ten particle size classes were counted, but for the analysis we performed for this study we used only the particles with equal spherical diameter (esd) of 90 and 108 μm. This was done because most elongate and slender fish larvae feed on prey that are between 20 and 50% of their mouth width (Stoecker and Govoni 1984; Hunter 1981; Theilacker and Dorsey 1980). We determined that mouth width (MW) was strongly correlated with total length (TL) in postemergent capelin larvae (MW = 0.03843TL + 0.03903; $r = 0.70$, $n = 62$). The average size of postemergent larvae is 5 mm (Taggart and Leggett 1984; Frank and Leggett 1982a). Therefore the appropriate prey size would range between 46 and 115 μm esd (see also Frank and Leggett 1986). The smallest size class counted (75 μm esd) was excluded, as it may have been undersampled by the 80-μm-mesh net.

Estimates of the total abundance of larval capelin in Bryants Cove during each sampling session were made by first summing the stratum density estimates at each grid station after multiplying by the respective stratum volume. Subsequently the abundance estimate at each grid station was corrected where applicable for bias due to diel migration below the 9-m maximum sampling depth and bias resulting from sampling only the 0- to 2-m stratum at the three outermost stations along the south side of the cove (see below). Finally the abundance estimates were summed over all stations.

Diel sampling conducted at station 10 on the transect (see Fig. 1) at 2-m depth-integrated intervals over a period of 19 h in 1982 and 48 h in 1983 revealed distinct vertical migration of postemergent capelin larvae over a depth range of 16 m (Fig. 2). The centre of distribution (the depth above which 50% of the sampled population was found) ranged over an average vertical distance of 7.2 m. Calculations of proportional depth distribution indicated that upwards of an additional 50% of the estimated larval populations sampled between 0 and 9 m could be found below 9 m during daylight hours. The migration patterns observed on these two specific occasions were consistent with the proportional depth distribution of larvae from all sampling sessions in 1981–83 at grid stations where sampling was performed to 9 m (Fig. 3). Although harmonic regression is generally used to model the observed diel pattern (Legendre and Legendre 1983), conditional time-based polynomial models were found to have greater predictive power and were therefore used to correct the systematic bias in the population estimates. Corrections were applied to the larval abundance estimates at the appropriate stations according to the time of sampling and the models illustrated in Fig. 4.

At times when only the six-station transect was sampled, multiple regression models of the relationship between larval density estimates from transect station-strata and estimates from grid station-strata were used to develop abundance estimates of the entire grid. These models were developed from data collected during 41 sessions when the 31 station-strata were sampled on the grid and were used to reconstruct abundance estimates for 27 sessions when only the 13 station-strata on the transect were sampled. All models were restricted to no more than 6 of the 13 station-strata density estimates, and model selection was made on the basis of Mallow's Cp statistic (see Hocking 1976). Each estimate retained was significant in its contribution to the regression at $p < 0.05$. The number of station-strata estimates in each model and the correlation coefficients for each are provided in Table 2. The average density for the "whole-cove" was calculated by dividing the sum of the station-strata absolute estimates by the sum of the station-strata volumes (cove volume). The relationship between the observed whole-cove average density and that estimated by the multivariate models (after independent diel bias correction) is provided in Fig. 5 ($r^2 = 0.96$, $n = 41$, $p < 0.0001$).

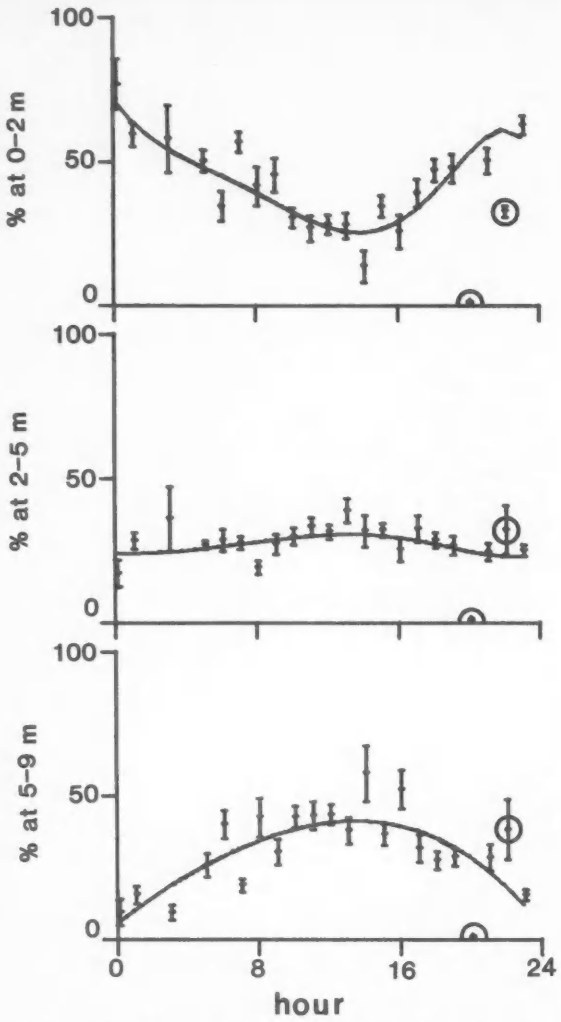

FIG. 3. Proportional diel depth distribution of capelin larvae from all sampling sessions in 1981, 1982, and 1983. Only data from stations where three depth strata (0–2, 2–5, 5–9 m) were sampled are included. The best fitting time-based polynomial joins the average percent (± 1 SE). A total of $N = 589$ samples make up the series. Circled averages indicate time points where $n < 3$.

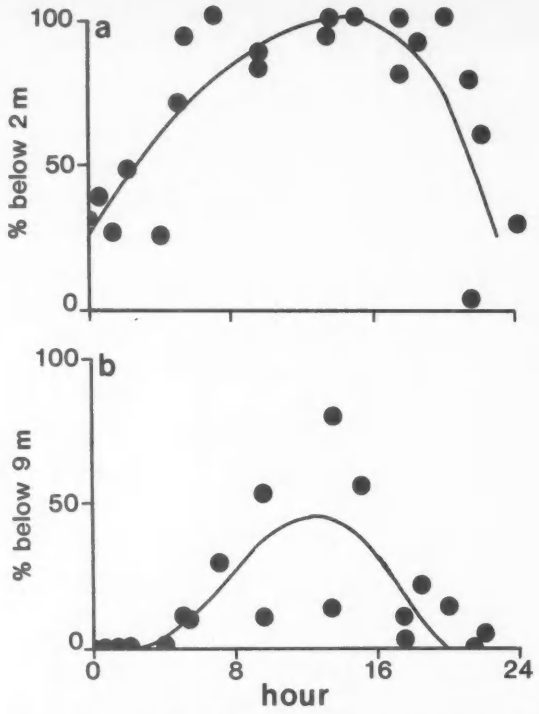

FIG. 4. Graphical description of the time-based polynomial functions fitted to the combined diel depth distributions of capelin larvae presented in Fig. 2. These models were used to correct for diel bias in the density estimates at (a) stations along the south side of the cove (see Fig. 1) where only the 0–2 m stratum was sampled and (b) deep stations where the depth exceeded 9 m.

As we were not concerned with eventually calculating mortality estimates of the plankton particle size classes, and as there was no systematic diel pattern in their vertical distribution, we simply estimated the average whole-cove density by calculating the geometric average of the density estimates from all station-strata sampled during each session.

Analyses

Relationships between the various physical and biological time-series were examined by spectral analyses using the ARIMA and SPECTRA procedures of SAS (1982) and the Spectral Analysis System (Cracker Version 1.011a) developed at the Bedford Institute of Oceanography. Spectral analysis is an analysis of variance approach to a time-series which is assumed to be a single realization of a stochastic process. In the analysis, the variance in the signal (the time based measure of wind, current, larval densities, plankton particle densities, etc.) around its mean is partitioned into contributions (the spectral density estimates) at frequencies which are harmonics of the length of the time-series. The analysis thus identifies those frequencies or periods where most of the variance in the signal is concentrated. The spectral estimates were multiplied by their corresponding frequency and plotted against the common logarithm of frequency to ensure that equal areas under the curve represented equal contributions to the total variance (Denman 1975). Cross-spectral analysis provided coherence spectra (the degree of mutual dependence between two signals at given frequencies) and phase spectra (the amount of shift or lag between the first and second signal). Statistical significance was assessed by splitting the time-series into 16 blocks of equal length with 50% overlap and performing spectral analysis on each. Fewer blocks decrease the statistical significance of the estimates, while a greater number limit the estimates to be calculated at only higher frequencies (shorter periods). Cross-spectral analysis between different physical variables was performed on the smoothed data. The lowpassed oceanographic time-series were used in the cross-spectral analysis with the biological variables. As a result of the frequency of biological sampling, only frequencies <1 cpd were considered.

TABLE 2. Number of independent transect station-strata estimates (N) and multiple correlation coefficient (R) for each multiple regression model used to predict larval density estimates of grid station-strata not on the transect ($n = 41$ for each model and all models had significant F statistics ($p < 0.0001$)).

Station	Stratum (m)	N	R
3	0–2	2	0.767
4	0–2	4	0.847
5	0–2	2	0.743
6	0–2	6	0.810
11	0–2	5	0.912
11	2–5	2	0.839
12	0–2	4	0.864
13	0–2	6	0.939
13	2–5	5	0.886
13	5–9	2	0.843
14	0–2	3	0.831
14	2–5	4	0.895
14	5–9	3	0.879
15	0–2	3	0.887
15	2–5	2	0.907
16	0–2	3	0.837
16	2–5	4	0.863
16	5–9	6	0.849

Results

Circulation Pattern

The circulation pattern in Bryants Cove was cyclonic in both the upper and lower strata of the water column and was consistent from year to year as shown by progressive vectors for each current meter (Fig. 6). The average current speed at each station was also consistent between years (Table 1). The average current measured further offshore at Station 4 in 1983 was predominantly north-eastward with an average speed of 11.3 cm/s (Fig. 6; Table 1). The depth-averaged speed on the inflow side of the cove (Station 3) was 4.95 and 4.65 cm/s in 1982 and 1983, respectively, and matched the depth-averaged speed on the outflow side of the cove (Station 2) in each year. The approximate flushing time of the cove calculated simply from the average circulation (4.8 cm/s) was 19 h.

Physical Relationships: Wind and Current

Comparison of time-series (both smoothed and lowpassed) of the U-components of wind (Fig. 7b) and current (Fig. 7a) measured at Station 4 in 1983 suggests strong correlation. The power spectra of each, and of wind stress in the onshore–offshore direction (t_x), indicate highest spectral density in the frequency bands centred at periods of 2.7 and 5.3 d (Fig. 8a, 8b). The maximum at 0.7 d in the current spectrum most probably reflects the inertial period (0.67 d) for this latitude, and the minor maximum at 1 d in the wind stress may reflect a sea breeze phenomenon. The two series (current$_u$ and t_x) were significantly coherent at these periods, with a smooth and slightly negative phase spectrum indicating a lagged current response to the wind (Fig. 9a, 9b). The coherence and phase spectra of wind$_u$ and current$_u$ were virtually identical. We suggest that at periods of 2–6 d the local currents are primarily wind driven. Analysis of the longshore wind–stress (t_y) revealed no significant coherence with either current component.

A comparison of temperature records for Bryants Cove (Station 4) and for Portugal Cove (24 km on the east side of

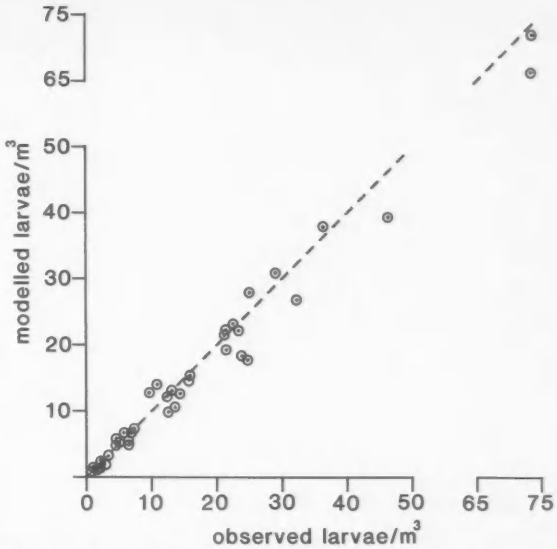

FIG. 5. Relationship between the observed and modelled whole-cove average density (total number per volume of cove). Modelled values were generated from multiple regression models (see Table 2) relating grid station estimates to transect station estimates. The slope of the relationship is not significantly different from 1.0 (broken line) and $r^2 = 0.96$ ($n = 41$, $p < 0.0001$).

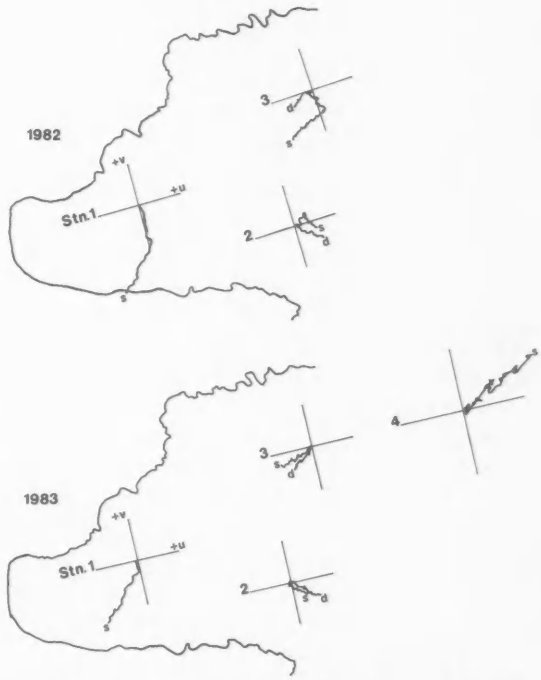

FIG. 6. Progressive vector diagrams of the smoothed current velocity for each of the deep (d) and shallow (s) instruments at each mooring station in Bryants Cove between June and August of 1982 and 1983. Positive U is oriented 54° east of north, and each axis from the origin represents 15 km. Note that Station 4 is not located at its true map position.

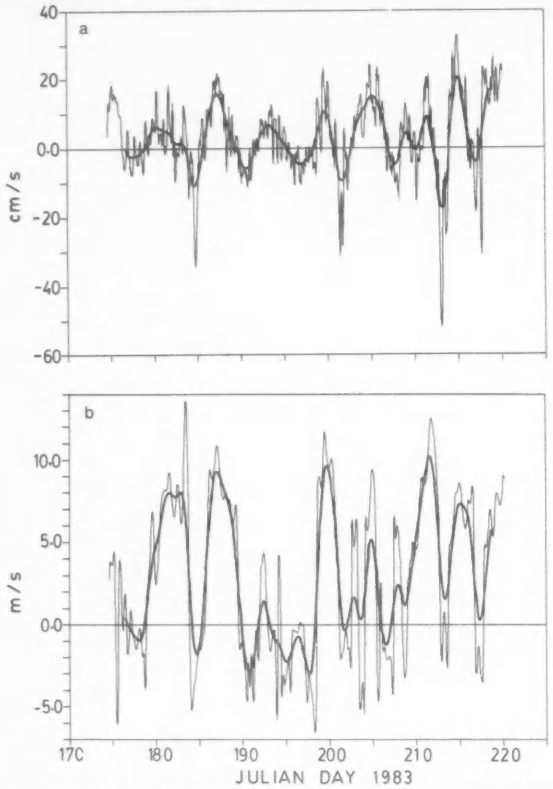

FIG. 7. Time-series (1983) of the smoothed and lowpassed (heavy line) hourly (a) current and (b) wind U-components (positive offshore; negative onshore). Wind data are from St. John's airport and current data are from Station 4 at 7 m depth.

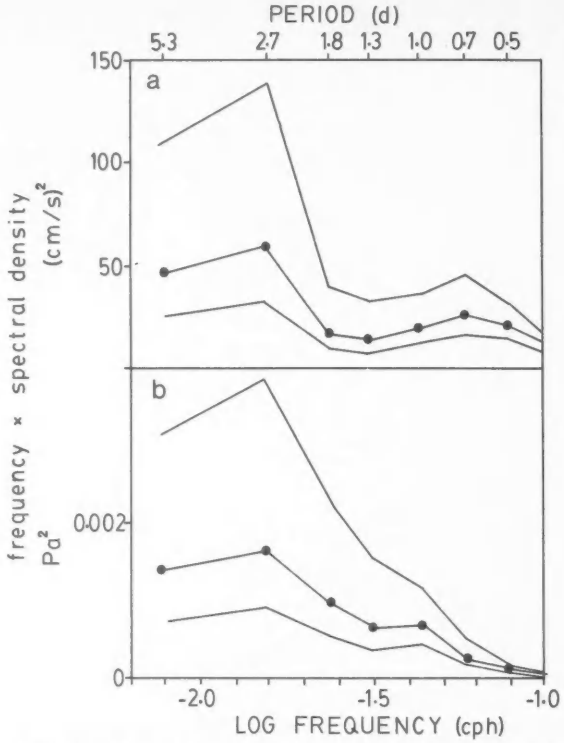

FIG. 8. Spectral density estimates of the (a) U-current and (b) wind stress (t_x). Spectral density estimates are bounded by 95% confidence intervals.

Conception Bay, Fig. 1) strongly suggests that the wind response is not a purely localized phenomenon (Fig. 10a, 10b). The two series were significantly coherent between 2- and 6-d periods, with a $-120°$ phase shift indicating a lagged (~4 h) inverse relationship (Fig. 11a, 11b). The same analysis conducted on data collected in 1982 showed similar results. In addition, both series mimic (inversely in the case of the east side temperature) the major oscillations seen in the wind and current signals shown in Fig. 7. Both temperature series were significantly coherent with t_x at 5.3 d ($-130°$ phase with Bryants Cove temperature and 0° phase with Portugal Cove temperature). There was no significant coherence between either temperature series and t_y. The above analyses conducted with wind stress and salinity and water density showed virtually identical results, illustrating that temperature is a good indicator of watermass and that wind stress in the onshore–offshore direction is responsible for watermass exchanges in the nearshore.

Biological Relationships: Larvae and Microzooplankton

Spectral analysis requires that a fixed sampling frequency is strictly maintained and that the resultant series is stationary (i.e. stable variance across the series). Neither requirement is typical of most biological data. As spectral analysis is reasonably robust against deviations from Gaussian assumptions (Koopmans 1974), the latter requirement is not a serious constraint, particularly if repeated spectral estimates are consistent (Denman 1975; Platt and Denman 1975). As the biological data were not evenly spaced in time, the observed larval and microzooplankton data series ($n = 68$ for each) were linearly interpolated, log transformed to improve stationarity, and smoothed using the lowpass filter to provide 1006 hourly estimates (Fig. 12a, 12b) which matched the physical data series. Interpolation per se is an acceptable procedure (Steven and Glombitza 1972; Legendre and Legendre 1983), however, the spectral estimates may be seriously biased when the number of "observations" in the interpolated series exceeds that of the original series. For this reason, analysis of the interpolated series proceeded as follows to assess the validity of the estimated variance spectrum and of using the interpolated series for cross-spectral analysis with the physical data:

(1) The interpolated series were analyzed in a manner similar to that of Steven and Glombitza (1972) by sampling each at 12-h intervals to provide a total of 84 evenly spaced observations from the 64 original observations. Spectral analysis was performed as above but without blocking because of the short length of the series. The resultant spectra shown in Fig. 13a and 13 b (for which there are no confidence interval estimates) reveal two distinct maxima in the larval series in the frequency bands centred at periods of 5.8 and 16–30 d. The microzooplankton series showed elevated spectral density between 3 and 8 d.

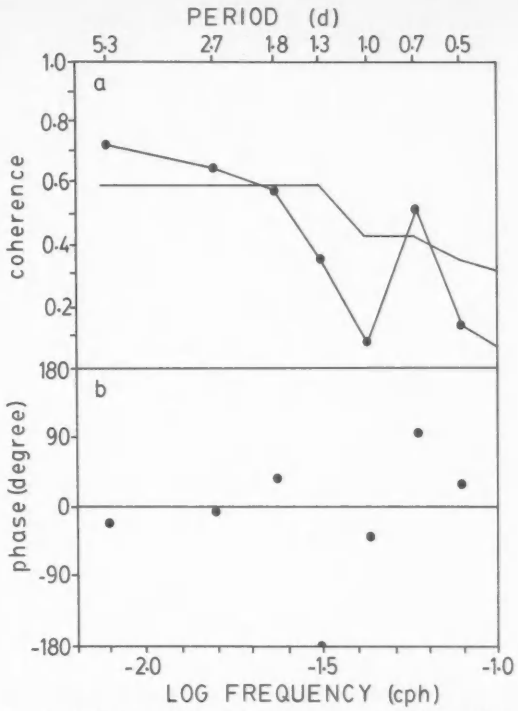

FIG. 9. (a) Coherence and (b) phase spectra of wind stress (t_x) and U-current. Significance for coherence ($p < 0.05$) is marked by the solid line.

(2) Spectral analysis was next performed on the two interpolated series with blocking as in the physical data. The resultant spectra (Fig. 14a, 14b) indicated significant spectral density at 2.7 and 5.3 d in both series. Blocking precluded longer period estimates. The apparent concordance at periods <6 d between spectra produced in the two analyses indicates that the interpolated series can be used for cross-spectral analysis with the physical data series, provided periods <1 d (the shortest biological sampling period) are excluded. This conclusion is further supported by the fact that the original biological data series were based on a non-uniform sampling interval which should greatly reduce the possibility of serious aliasing (Denman 1975) and the fact that during periods of onshore winds and pronounced larval emergence (and increased variation over time), the biological sampling frequency was increased from 1/d to between 3 and 4/d. Consequently the interpolated data series for both larvae and microzooplankton were used in subsequent analyses.

Although the larval and microzooplankton series had similar spectral density distributions and were in phase, there was no significant coherence at periods >1 d. This result is important, as it indicates that while the two signals varied together at similar frequencies (in phase), their respective amplitudes did not vary together, i.e. increases or decreases in larval density were not proportional to increases or decreases in plankton particle density. The higher amplitude fluctuations in the larval series relative to the plankton particle series are evident in Fig. 12. The 16-d maximum evident in the first larval spectrum was conspicuously absent from the microzooplankton spectrum (Fig. 13).

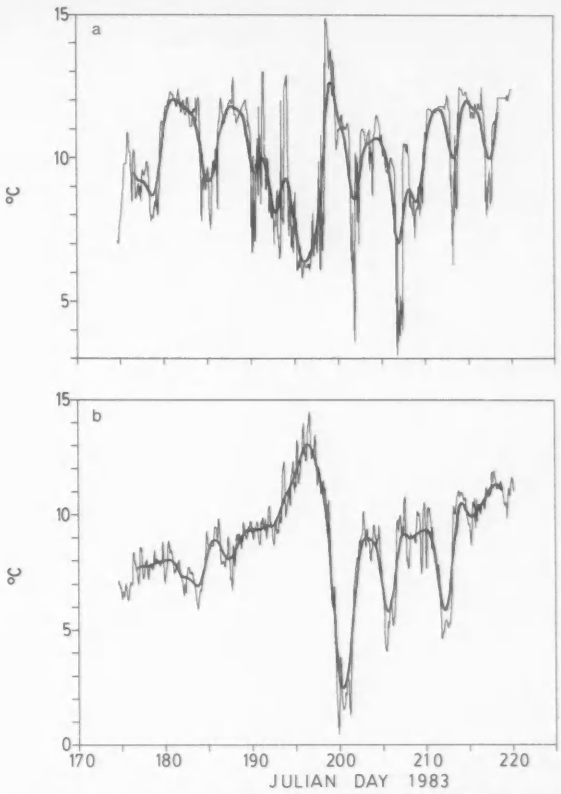

FIG. 10. Time series of temperatures recorded in 1983 at (a) Portugal Cove on the east side of Conception Bay and (b) Bryants Cove on the west side of the bay, 25 km distant from Portugal Cove. (Portugal Cove records provided by D. Keats, Memorial University of Newfoundland).

Physical–Biological Relationships

The major pattern emerging from the independent spectral analyses of both the physical and biological time-series is one of recurrent spectral maxima at periods of between 3 and 6 d. Cross-spectral analysis resolved significant coherence between the larval capelin series and t_x at 5.3 d (Fig. 15a). Furthermore, the phase spectrum (Fig. 15b) showed a 130° shift demonstrating a lagged inverse relationship (increased onshore wind stress leading an increased larval density). The larval series was also significantly coherent with the U-components of wind and current at the same period and showed similar phase relationships. There was no significant coherence between the larval series and any of the other physical variables.

Cross-spectral analysis of the microzooplankton and physical data series determined marginal coherence with t_x (and U-wind) at 5.3 d and had a similar phase relationship as seen with the larval series. Microzooplankton variations were coherent with temperature at Bryants Cove at periods of 3–6 d with a near-zero phase (Fig. 16). Almost identical coherence spectra were derived from cross-spectral analysis of the microzooplankton with salinity, density, and with temperature measured at Portugal Cove. This result is not unexpected given the previously described coherence between these variables and

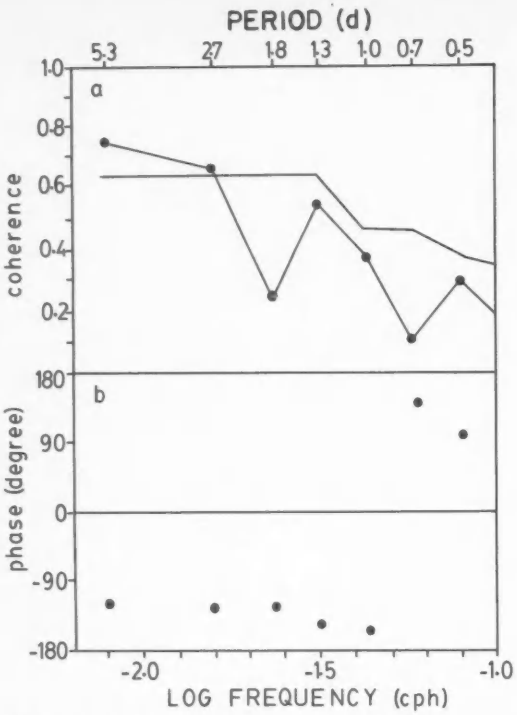

FIG. 11. (a) Coherence and (b) phase spectra for the temperature time-series illustrated in Fig. 10. Significance for coherence is marked by the solid line ($p < 0.05$).

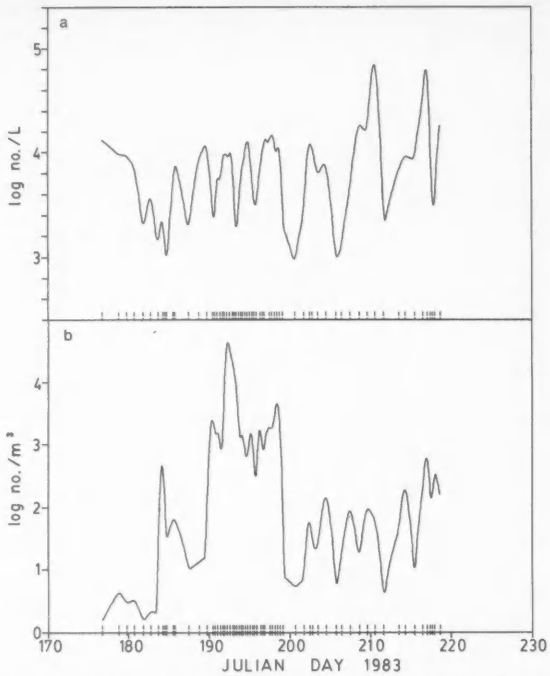

FIG. 12. 1983 time series of log-transformed (a) 90–108 μm esd microzooplankton particles (whole-cove average density) and (b) capelin larvae (whole-cove average density) generated from a filtered hourly linear interpolation of the 68 observed estimates. Times when the observed estimates were made are marked on the date axis.

temperature measured at Bryants Cove. Microzooplankton were not significantly coherent with any other physical variables.

Discussion

Development of the Biological Data

Legendre and Demers (1984) have suggested that probing the significant scales of variation in dynamic biological oceanography and limnology will require the merging of horizontal and vertical studies in an integrated approach and the design and application of new sampling techniques and schemes. The methodology and results reported here indicate that a time-series of larval population estimates within a small and well-defined region can be obtained with good spatial and temporal resolution. In addition we have shown that statistically significant estimates of population size can be derived from multiple regression models incorporating a limited number of spatial density estimates (i.e. grid estimates from single transect observations), thereby greatly reducing the sampling effort. In the particular case we considered, the level of statistical significance of the models developed is likely a function of the point source of larvae at the head of the cove and the cove circulation. The seasonally cyclonic current pattern in the cove is such that the current sets landward on the northern half of the sampling grid and seaward on the sourthern half, each with equivalent average flow. The sampling transect was thus located just south of, and parallel to, the region where the current bends from inflowing to outflowing. This appears to have caused the majority of larvae to be transported from their source on the beach to beyond the cove boundaries along the transect. This interpretation is supported by the fact that the best multiple regression models for estimating larval density in the cove relied on transect estimates. Furthermore, a series of dye diffusion–advection studies (not presented) showed the centre of mass of dye concentration to be advected seaward along the transect. These findings suggest that many of the logistic difficulties inherent in plankton surveys could be surmounted, without a significant loss of information, by the prior development of statistical models relating total area densities to densities on reduced sampling grids. This will require that sufficient effort be expended initially to define the distribution pattern in detail and to concurrently define the physical processes responsible for determining the pattern so that the appropriate stations can be chosen. We caution that this approach may prove useful only in lakes, embayments, and offshore banks which have predictable and dominant circulation features.

The systematic sampling approach we employed precludes statistical error estimation which would be possible had a randomized sampling design been employed. However, given the need to integrate samples both vertically and horizontally on a short time scale in order to deal with horizontal and vertical differences in current velocity and with diel vertical movements, randomized designs are likely to quickly become logistically impossible and to be less precise. We believe the approach adopted represents a viable compromise between error estimation and the need for synoptic high resolution on

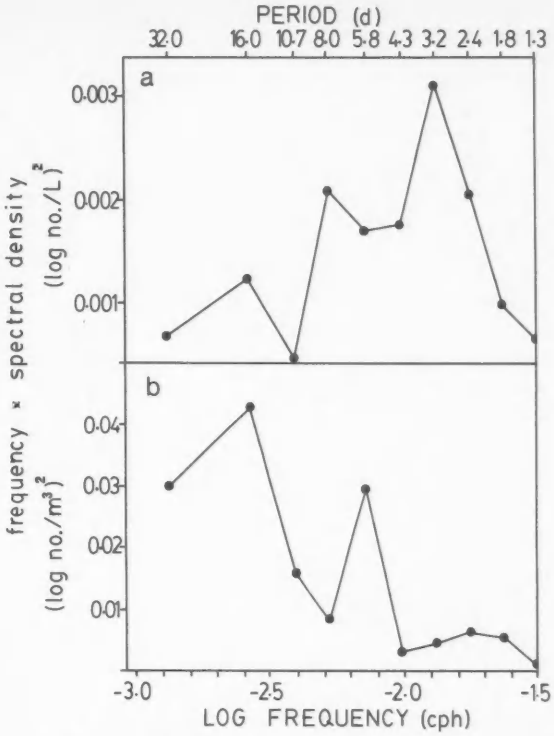

FIG. 13. Spectral density of (a) microzooplankton density and (b) capelin larvae density derived from sampling the interpolated series (Fig. 12) at 12-h intervals for a total of 84 "observations."

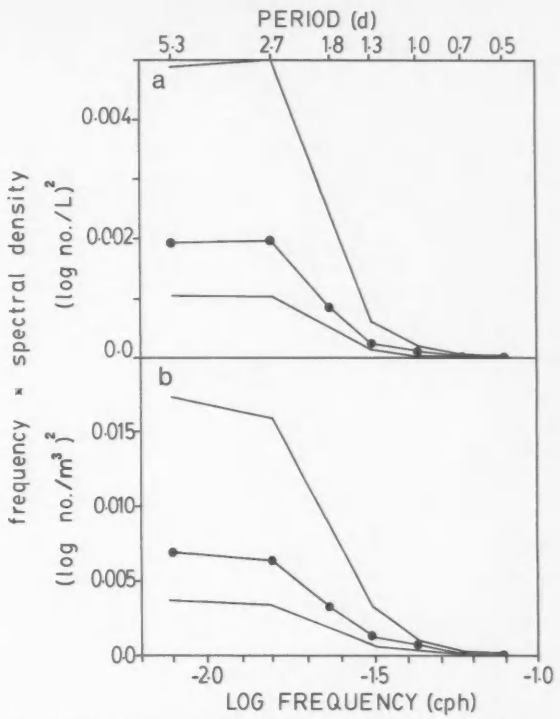

FIG. 14. Spectral density estimates of (a) microzooplankton density and (b) capelin larvae density time-series illustrated in Fig. 12. Spectral densities are bounded by 95% confidence intervals.

the horizontal and vertical scale in order to achieve precise estimates of abundance. The viability of the approach is strengthened by the fact that the population estimates of larvae derived using this method, and those from simple geometric average densities, were highly correlated ($r^2 = 0.89$, $n = 41$, $p < 0.0001$) and had both slope and intercept values not significantly different from 1.0 and 0.0, respectively.

A further advantage of the pump sampling method and the systematic sampling design employed is that they allowed for synoptic estimates of both larval and plankton particle concentrations at precisely the same time and place with a horizontal scale resolution of 200 m, a vertical scale resolution of 2–4 m, and a temporal resolution of 6–8 h. This type of resolution is necessary if the various larval/food survival hypotheses (see the introduction) are to be rigorously tested. The physical–biological relationships identified by spectral analysis at higher frequencies (periods of 3–6 d) are unlikely to be resolved with a low-frequency broad-scale sampling programme.

The vertical resolution achieved by our design also permitted resolution of diel vertical migrations of yolk-sac larvae at a scale even smaller than that reported by Fortier and Leggett (1983), who noted the ecological significance of this behaviour in terms of feeding success and rate and direction of advective transport. Such resolution of diel migratory patterns allows it to be satisfactorily modelled in a purely empirical manner. These models can then be used to correct for biases in population estimates introduced by larval behaviour and sampling problems related to logistics and bathymetry. It is because of these biases that large-scale programmes have wisely employed bottom-to-surface integrated sampling. However, such methods eliminate all possibility of relating larval and food density distributions to each other and to the physical regime at relevant scales. The consistent and systematic diel vertical migrations exhibited by immediate postemergent capelin larvae contradict the earlier assumptions made by Fortier and Leggett (1982) and Frank and Leggett (1982b) that the yolk-sac larvae can be considered passive contaminants on the vertical scale and are therefore subject to extensive vertical mixing. The failure of this assumption to be met (also recognized by Fortier and Leggett 1983) can lead to significantly biased estimates of population size through slight differences in the time and depth of sampling, particularly if sampling occurs when larvae are migrating at their greatest rate. Our model (Fig. 4) for correcting migration bias has room for improvement. However, analysis of all the data was consistent with the model and suggests that although bias was not totally accounted for, it was much reduced.

It is equally possible to bias the change in population size through changes in sampling frequency. We infer from our calculation that cove flushing could occur within 24 h that the probability of sequentially sampling the same population is severely reduced if sampling frequency is less than once per day. Both of the above potential biases highlight the influence of inappropriate temporal and spatial scales when working in a dynamic environment. Frequent sampling of larvae following wind-driven emergence in 1983 revealed declines in larval density of more than an order of magnitude in periods as short

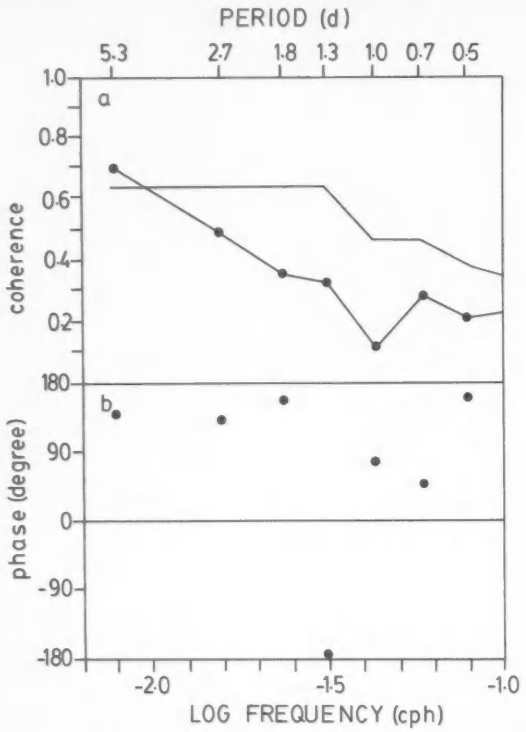

FIG. 15. (a) Coherence and (b) phase spectra of cross-shore wind stress (t_x) and capelin larvae density. Significance for coherence is marked by the solid line ($p < 0.05$).

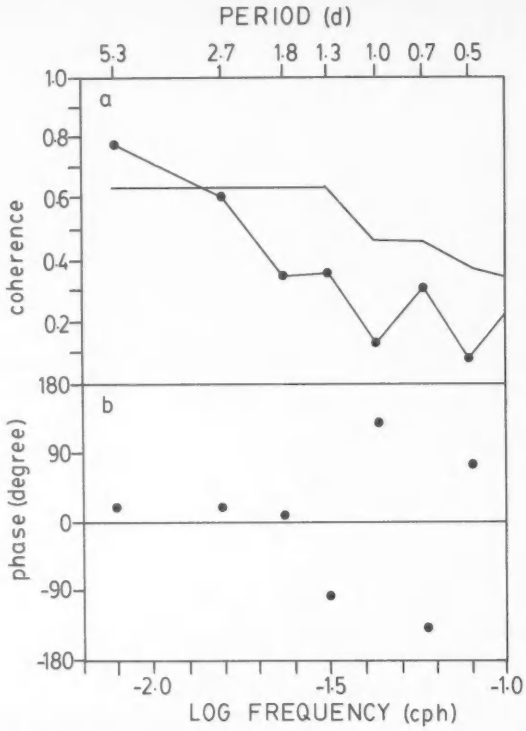

FIG. 16. (a) Coherence and (b) phase spectra of temperature and microzooplankton. Significance for coherence is marked by the solid line ($p < 0.05$).

as 6–8 h. These data indicate that the proportion of larval loss attributable to advection, as opposed to mortality, is considerable. Having developed the diel correction models, it is a relatively straightforward but nontrivial task to incorporate the migratory behaviour of the larvae, their population distribution at a given time, and the simultaneously determined current velocity data to calculate measures of advective loss (emigration) and realized mortality. The results of this work are forthcoming.

Watermass Exchange Hypothesis

Templeman (1966) proposed a coastal watermass exchange phenomenon to explain intraseasonal variation in the nearshore abundance of cod on the eastern coast of Newfoundland. The hypothesis called for the intermittent presence, in the nearshore, of warm surface water and cold subthermocline water. He further hypothesized the watermass exchanges to be wind-driven. Frank and Leggett (1982b) adopted Templeman's hypothesis to explain temporal variation in nearshore temperature changes and related changes in larval fish and zooplankton abundance. It was further demonstrated that the short-term nearshore temperature fluctuations were generally synchronous along the eastern coast of Newfoundland (Leggett et al. 1984), implying a large-scale phenomenon. Spectral analyses of the time-series of wind and current in the nearshore areas of Conception Bay in 1983 are fully consistent with the watermass exchange hypothesis and leave little doubt that the nearshore currents, and related temperature, salinity, and density, respond to wind forcing at periods ranging from 3 to 6 d.

Our finding that the longshore wind component (V) showed no coherence with current and temperature oscillations is at odds with the more general observation that longshore winds drive offshore surface water excursions and coastal upwelling. We attribute our findings in part to the angle (54°) around which we resolved the data. The main axis (longshore) for Conception Bay is ~25° and therefore closely corresponds to the cross-shore axis of Bryants Cove. Thus the hydrodynamics in the cove may be responding more directly to the large-scale effects of wind on Conception Bay. This interpretation is supported by the dominant large-scale longshore wind effects on Trinity Bay documented by Yao (1986).

The physical–biological cross-spectral analyses showed larval abundance oscillations to be coherent with wind and current at periods of ~5 d. The abundance oscillations of microzooplankton concentration, although marginally coherent with cross-shore wind forcing, showed greater coherence with temperature. These observations demonstrate a greater biological significance of the watermass exchange hypothesis than suggested by Templeman (1966) and support the speculation of Leggett et al. (1984) that water temperature influences early larval survival through a more direct influence on food production. However, our analyses also demonstrate that although larvae and their potential prey oscillate in synchrony with wind, currents, and temperature, they are not proportionally related to each other. This finding implies that various levels of

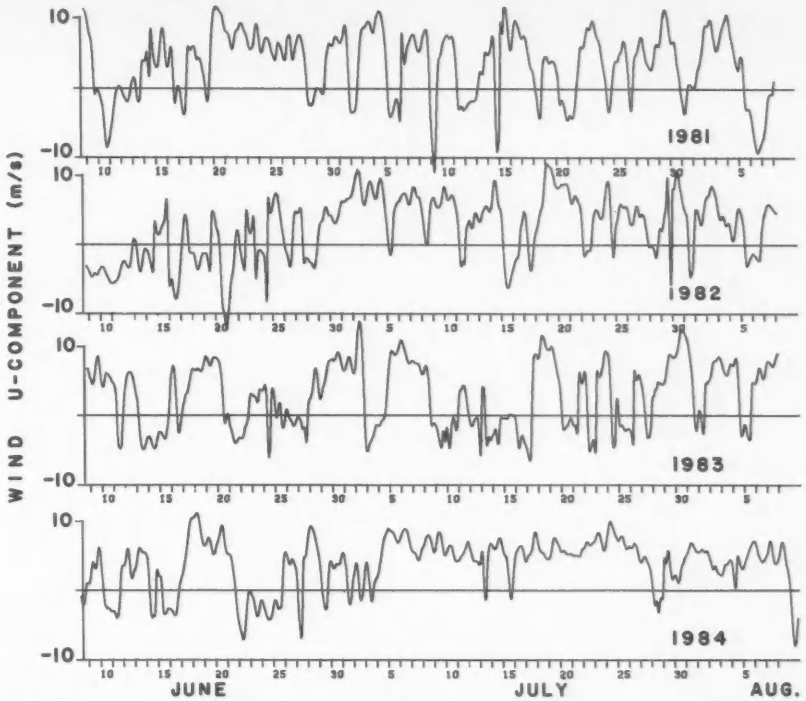

FIG. 17. Time-series of smoothed wind U-component at St. John's airport for June and July of 1981–84.

elevated food concentrations can be coincident with high concentrations of larvae.

The spectral maxima in larval density at 16–30 d in the first spectral analysis (Fig. 13b) appears to be related to capelin spawning and hatching periodicity. In 1983, capelin spawned on the beach at Bryants Cove between 15 and 21 June (heaviest on 18, 20, and 21) and again on 20, 21, and 24 July, a spawning interval of 30 d. The time to median hatching varies between 9 and 13 d in the high-tide zone and between 18 and 24 d in the low-tide zone (Frank and Leggett 1981a, 1981b). This range of incubation periods will result in a median hatching period of 16 d. The absence of spectral maxima at these periods in the microzooplankton abundance supports our interpretation.

The conclusions drawn from the spectral analysis of the biological data and the cross-spectral analysis of that data with the physical data are necessarily deficient due to our necessary interpolation of the biological data. We do, however, believe them to be essentially correct for the several reasons given under Biological Relationships: Larvae and Microzooplankton.

Implications of Watermass Exchange Variability

The influence of cross-shore wind forcing, and the watermass exchange which results, on the nearshore biological community structure is significant. The importance of the frequency of onshore wind events to capelin larvae derives from the fact that the majority of larvae resident in beach sediments have depleted their yolk sac within a 4- to 7-d posthatch window, beyond which their physical condition is severely affected (Frank and Leggett 1982a). This relatively short period for successful larval emergence led Frank and Leggett (1982b) to analyze the St. John's wind field over a period of 20 yr. They calculated the average number of days of prevailing offshore winds to be 24.1 (SD = 2.9) and 26.8 (SD = 3.0) for June and July, respectively. Assuming that onshore winds endure for an average of ~24 h, the average frequency of onshore winds would be once every 6.3 d for both months combined. The concordance between average onshore wind frequency and viable posthatch beach residence time for larvae led to the argument that early summer beach spawning was adaptive (Frank and Leggett 1983a, 1983b). However, we found that by considering ± 1 SD in the calculation of the 20-yr average, a much greater range of onshore wind frequencies emerged (every 3.4–25.8 d), demonstrating that there is considerable interannual variation in onshore wind frequency and hence in the "matching" of the emergence "window" (4.2–6.7 d). Time-series of the U-component (onshore–offshore) of the wind field for June and July of 1981–84 detail the extreme variability in periodicity, strength, and duration of onshore-offshore wind oscillations among years (Fig. 17). It is readily apparent on inspection that in 1981 and 1983, onshore winds were stronger, more frequent, and of greater duration than in 1982 and 1984. This was particularly true in the latter part of each record when the majority of capelin hatching and emergence took place. Integration of the onshore wind component (scaled to a constant 10 m/s onshore wind) for the period of 25 June to 7 August measured 0.148, 0.104, 0.120, and 0.059 for 1981–84, respectively. Spectral analyses of these same signals revealed spectral maxima between 5.5 and 6.0 d in all but the 1984 spectrum (Fig. 18). This is consistent with the earlier analyses of onshore wind intervals. However, the proportion of variation in the wind signal found at these periods was itself extremely variable among years. There were dominant and

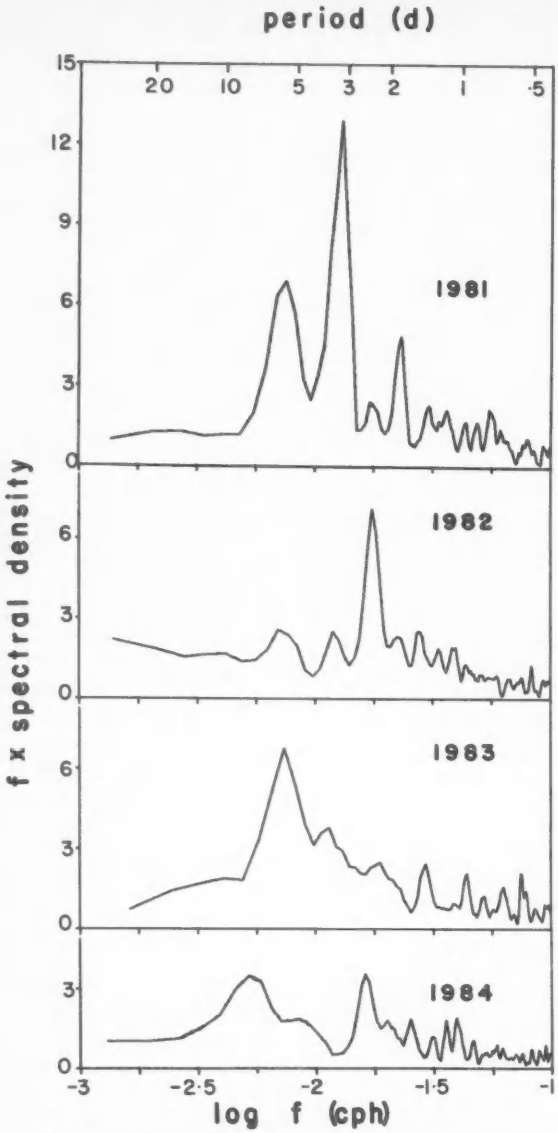

FIG. 18. Spectral densities of time-series of wind U-components illustrated in Fig. 17.

sharp maxima in the 1981 spectrum at periods of 1.8, 3.2, and 5.6 d. In comparison, the 1982 spectrum was less sharp and weak, while the 1983 spectrum was very broad and relatively strong. The 1984 spectrum was particularly broad and weak, reflecting the virtual absence of onshore winds during the latter two thirds of the signal when the majority of larvae were ready to emerge. Integration measures of the spectra between periods of 1 and 7.4 d (scaled to a broad-band unit spectrum) were 0.230, 0.133, 0.179, and 0.089 for 1981–84, respectively. The scaled integrals of the onshore U-component and of the spectra were significantly correlated ($r^2 = 0.95$, $n = 4$, $p < 0.05$), suggesting that either method can be used as a composite measure of onshore wind frequency, magnitude, and duration. The generally declining frequency and intensity of onshore winds and watermass exchange during the critical larval emergence period over the years 1981–84 lead us to hypothesize that the strength of capelin year classes hatched in these years (assuming equal spawning biomass) should also generally decline from 1981 to 1984. We plan to test this hypothesis using either the U-component or spectral integrals of annual summer wind data and year class strength data for capelin (with an appropriate discounting for spawning biomass) in an effort to test and perhaps improve the Leggett et al. (1984) recruitment model for possible application to stock management.

Acknowledgments

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References

BAILEY, K. M. 1981. Larval transport and recruitment of Pacific hake *Merlucius productus*. Mar. Ecol. Prog. Ser. 6: 1–9.

BLAXTER, J. H. S. [ED] 1974. The early life history of fish. Springer-Verlag, New York, NY. 765 p.

CUSHING, D. H. 1972. The production cycle and the numbers of marine fish. Symp. Zool. Soc. Lond. 29: 213–232.

1975. Marine ecology and fisheries. Cambridge University Press, London. 278 p.

DAHLBERG, M. D. 1979. A review of survival rates of fish eggs and larvae in relation to impact assessments. Mar. Fish. Rev. 41: 1–12.

DENMAN, K. L. 1975. Spectral analysis: a summary of the theory and techniques. Environ. Can. Fish. Mar. Serv. Tech. Rep. 539: 27 p.

FORMAN, M. G. 1978. Manual for tidal currents analysis and predictions. Pac. Mar. Sci. Rep. 78-6. Institute of Ocean Sciences, Patricia Bay, Sydney, B.C. 70 p.

FORTIER, L., AND W. C. LEGGETT. 1982. Fickian transport and dispersal of larvae in estuaries. Can. J. Fish. Aquat. Sci. 39: 1150–1163.

1983. Vertical migrations and transport of larval fish in a partially mixed estuary. Can. J. Fish. Aquat. Sci. 40: 1543–1555.

1984. Small-scale covariability in the abundance of fish larvae and their prey. Can. J. Fish. Aquat. Sci. 41: 502–512.

1985. A drift study of larval fish survival. Mar. Ecol. Prog. Ser. 25: 245–257.

FRANK, K. T., AND W. C. LEGGETT. 1981a. Wind regulation of emergence times and early larval survival in capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. 38: 215–223.

1981b. Prediction of egg development and mortality rates in capelin (*Mallotus villosus*) from meteorological, hydrographic, and biological factors. Can. J. Fish. Aquat. Sci. 38: 1327–1338.

1982a. Environmental regulation of growth rate, efficiency, and swimming performance in larval capelin (*Mallotus villosus*) and its application to the match/mismatch hypothesis. Can. J. Fish. Aquat. Sci. 39: 691–699.

1982b. Coastal water mass replacement: its effect on zooplankton dynamics and the predator–prey complex associated with larval capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. 39: 991–1003.

1983a. Multispecies larval fish associations: accident or adaptation? Can. J. Fish. Aquat. Sci. 40: 754–762.

1983b. Survival value of an opportunistic life stage transition in capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. 40: 1442–1448.
1986. Effect of prey abundance and size on the growth and survival of larval fish: an experimental study employing large volume enclosures. Mar. Ecol. Prog. Ser. 34: 11–22.

GODIN, G. G. 1972. The analysis of tides. University of Toronto Press, Downsview, Ont. 264 p.

GULLAND, J. A. 1965. Survival of the youngest stages of fish, and its relation to year-class strength. ICNAF Environ. Symp. Spec. Publ. 6: 363–371.

HENDERSON, P. A., J. W. WHITEHOUSE, AND G. H. CARTWRIGHT. 1984. The growth and mortality of larval herring, *Clupea harengus* L., in the River Blackwater Estuary, 1978–1980. J. Fish. Biol. 24: 613–622.

HEWITT, R. P., G. H. THEILACKER, AND N.C.H. LO. 1985. Causes of mortality in young jack mackerel. Mar. Ecol. Prog. Ser. 26: 1–10.

HJORT, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Reun. Cons. Inst. Explor. Mer 20: 1–228.

HOCKING, R. R. 1976. The analysis and selection of variables in linear regression. Biometrics 32: 1–50.

HUNTER, J. R. 1981. Feeding ecology and predation of marine fish larvae, p. 33–77. *In* R. Lasker [ed.] Marine fish larvae. University of Washington Press, Seattle, WA. 131 p.

JOHN, H-C. 1984. Drift of larval fishes in the ocean: results and problems from previous studies and a proposed field experiment, p. 39–59. *In* J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill [eds.] Mechanisms of migrations in fishes. Plenum Press, New York, NY. 574 p.

KOOPMANS, L. H. 1974. The spectral analysis of time series. Academic Press, New York, NY. 366 p.

LASKER, R. 1975. Field criteria for the survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull. U.S. 73: 453–462.

LEGENDRE, L., AND S. DEMERS. 1984. Towards dynamic biological oceanography and limnology. Can. J. Fish. Aquat. Sci. 41: 2–19.

LEGENDRE, L., AND P. LEGENDRE. 1983. Numerical ecology. Elsevier Scientific Publ. Co., Oxford. 419 p.

LEGGETT, W. C., K. T. FRANK, AND J. E. CARSCADDEN. 1984. Meteorological and hydrographic regulation of year-class strength in capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. 41: 1193–1201.

NELSON, W., M. C. INGHAM, AND W. E. SCHAAF. 1977. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus*. Fish. Bull. U.S. 75: 23–42.

NORCROSS, B. L., AND R. F. SHAW. 1984. Oceanic and estuarine transport of fish eggs and larvae: a review. Trans. Am. Fish. Soc. 113: 153–165.

PEARCY, W. G. 1962. Ecology of an estuarine population of winter flounder, *Pseudopleuronectese americanus* (Walbum). II. Distribution and dynamics of larvae. Bull. Bingham. Oceanogr. Collect. Yale Univ. 18: 16–38.

PLATT, T., AND K. L. DENMAN. 1975. Spectral analysis in ecology. Annu. Rev. Ecol. Syst. 6: 189–210.

ROTHLISBERG, P. C. 1982. Vertical migration and its effect on dispersal of penaeid shrimp in the Gulf of Carpentaria, Australia. Fish. Bull. U.S. 80: 541–554.

SAS. 1982. SAS/ETS: econometrics and time series library. SAS Institute Inc., Box 8000, Cary, NC 27511. 398 p.

SHARP, G. D. 1980. Report of the workshop on effects of environmental variation on survival of larval pelagic fishes, p. 15–63. *In* G. D. Sharp [ed.] Workshop on the effects of environmental variation on the survival of larval pelagic fishes. Intergovernmental Oceanographic Commission Workshop Rep. No. 28, Unesco, FAO, Rome. 323 p.

SINCLAIR, M., M. J. TREMBLAY, AND P. BERNAL. 1985. El Niño events and variability in a Pacific mackerel (*Scomber japonicus*) survival index: support for Hjort's second hypothesis. Can. J. Fish. Aquat. Sci. 42: 602–608.

SMITH, P. E. 1978. Biological effects of ocean variability: time and space scales of biological response. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 173: 117–127.
1981. Fisheries on pelagic schooling fish, p. 2–31. *In* R. Lasker [ed.] Marine fish larvae: morphology, ecology and relation to fisheries. University of Washington Press, Seattle, WA. 131 p.

SMITH, S. D., AND E. G. BANKE. 1975. Variation of the sea surface drag coefficient with wind speed. Q. J. R. Meteorol. Soc. 101: 665–673.

STEVEN, D. M., AND R. GLOMBITZA. 1972. Oscillatory variation of a phytoplankton population in a tropical ocean. Nature (Lond.) 237: 105–107.

STOECKER, D. K., AND J. J. GOVONI. 1984. Food selection by young larval menhadden (*Brevootia patronus*). Mar. Biol. 80: 299–306.

TAGGART, C.T., AND W. C. LEGGETT. 1984. Efficiency of large-volume plankton pumps, and evaluation of a design suitable for deployment from small boats. Can. J. Fish. Aquat. Sci. 41: 1428–1435.

TEMPLEMAN, W. 1966. Marine resources of Newfoundland. Bull. Fish. Res. Board Can. 154: 170 p.

THEILACKER, G., AND K. DORSEY. 1980. Larval fish diversity, a summary of laboratory and field research, p. 105–142. *In* G. D. Sharp [ed.] Workshop on the effects of environmental variation on survival of larval pelagic fishes. Intergovernmental Oceanographic Commission Workshop Rep. No. 28, Unesco, FAO, Rome. 323 p.

TILSETH, S., AND B. ELLERTSEN. 1984. The detection and distribution of larval Arcto–Norwegian cod, *Gadus morhua*, food organisms by an *in situ* particle counter. Fish. Bull. U.S. 82: 141–156.

WARE, D. M., AND T. C. LAMBERT. 1985. Early life history of Atlantic mackerel (*Scomber scombrus*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 42: 577–592.

WHITEHEAD, H., AND J. E. CARSCADDEN. 1985. Predicting inshore whale abundance — whales and capelin off the Newfoundland coast. Can. J. Fish. Aquat. Sci. 42: 976–981.

YAO, T. 1986. The response of currents in Trinity Bay, Newfoundland, to local wind forcing. Atmos. Ocean 24: 235–252.

Physiological Changes during Seaward Migration of Wild Juvenile Coho Salmon (*Oncorhynchus kisutch*)

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Rodgers, J. D., R. D. Ewing, and J. D. Hall. 1987. Physiological changes during seaward migration of wild juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 44: 452–457.

Peaks in migration of wild juvenile coho salmon (*Oncorhynchus kisutch*) from Knowles Creek (Siuslaw River, Oregon) occurred in November and May. Condition factor of nonmigrant fish was higher than migrants or captives throughout the study. Skin guanine levels of migrant fish rose sharply during the first 2 wk of April and continued to rise through June. Gill (Na + K)-ATPase specific activity of migrants rose gradually from a low in January to a maximum in June. Gill (Na + K)-ATPase activity of migrants and nonmigrants was low and not significantly different during November to mid-March. During April, however, gill ATPase activity of migrants rose to become significantly higher than that of nonmigrants until the first 2 wk of May. Cyclic changes in gill (Na + K)-ATPase activity was not observed in these fish. Gill (Na + K)-ATPase activity of fish reared in a laboratory was similar to that of wild nonmigrants until it peaked during the last 2 wk of April, after which the specific activity was lower than either migrants or nonmigrants.

Chez le saumon coho (*Oncorhynchus kisutch*) juvénile sauvage, les pointes de la dévalaison dans le ruisseau Knowles (rivière Siuslaw, Orégon) ont eu lieu en novembre et mai. Le coefficient de condition des poissons non migrateurs a été plus élevé que celui des saumons migrateurs ou captifs pendant toute l'étude. Chez les poissons migrateurs, les teneurs en guanine de la peau ont nettement augmenté au cours des 2 premières sem d'avril et cette augmentation s'est poursuivie jusqu'en juin. L'activité spécifique du (Na + K)-ATPase dans les ouies de ces poissons est graduellement passée d'un faible niveau en janvier à un maximum en juin. Chez les saumons migrateurs et non migrateurs, l'activité du (Na + K)-ATPase dans les ouies était faible; de plus, elle n'était pas nettement différente de novembre à la mi-mars. Toutefois, en avril, l'activité de l'ATPase dans les ouies des migrateurs est devenue nettement supérieure à celle des non-migrateurs jusqu'aux 2 premières sem de mai. Aucune variation cyclique de l'activité du (Na + K)-ATPase dans les ouies n'a été observée chez ces derniers. Cette fonction était semblable chez les poissons élevés en laboratoire et les non-migrateurs sauvages jusqu'à ce qu'elle atteigne une pointe au cours des 2 dernières sem d'avril, après quoi l'activité spécifique était inférieure à celle observée chez les migrateurs et les non-migrateurs.

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Anadromous salmonids begin juvenile life in rivers and streams and then migrate to the sea where they complete their growth and development. Prior to and during development of the migratory urge, the juveniles undergo a myriad of behavioral, morphological, and physiological changes so that the transition from fresh to saltwater can be made (Folmar and Dickhoff 1980). However, there are few studies relating behavioral aspects of migration with physiological changes that occur during smolting, especially under conditions where these changes have not been modified by previous fish culture. While seaward migration is assumed to be associated with the smolting process, other types of migrations not related to the seaward migration of smolts have been documented (e.g. Chapman 1962; Mason 1975; Cederholm and Scarlett 1981; Hartman et al. 1982).

This paper examines some physiological changes associated with smolting in coho salmon (*Oncorhynchus kisutch*) during the migration of a population of wild juveniles from Knowles Creek, a tributary of the Siuslaw River, Oregon. Specifically, the objectives of this study were to (1) determine the timing and magnitude of migration of juvenile coho out of the watershed, (2) examine changes in condition factor, skin guanine levels, and gill (Na + K)-ATPase activity between migrating, nonmigrating, and captive groups of Knowles Creek juvenile coho,

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(3) relate these changes in smolt indices to the timing of migration, and (4) examine the relation between skin guanine levels, gill (Na + K)-ATPase activity, and fish fork length.

Methods

Knowles Creek is a fifth-order tributary of the Siuslaw River in Oregon's central Coast Range. The stream heads at an elevation of 950 m and drains 58 km^2 of highly erodable Tyee Sandstone formation before flowing into tidewater of the Siuslaw River at Mapleton, Oregon, approximately 19 river km from the Pacific Ocean.

Stream discharge was monitored with a continuous water level recorder installed near the mouth of Knowles Creek. Standard hydrological techniques (Chow 1964) were used to determine stream discharge at various water levels and the resulting stream discharge relationship was used to convert average daily water levels to stream discharge in cubic metres per second. A Partlow chart thermograph located near the water level recorder was used to measure stream temperature continuously.

In mid-October 1983, 100 juvenile coho were collected from Knowles Creek, transported to laboratory facilities in Corvallis, held in a circular tank 0.91 m in diameter and 0.78 m deep supplied with 13°C well water, and fed Oregon Moist Pellet ad libitum daily. Once in January, February, March, and June and semimonthly in April and May, 20 randomly sampled fish were anesthetized with tricaine methane sulfonate (MS222), weighed to the nearest 0.1 g, and measured to the nearest millimetre fork length. Condition factor for each sampled fish was determined with the formula KFL = (weight × length^{-3}) × 10^5. A small sample of gill filaments was carefully clipped from each of the 20 fish by the method of Zaugg and McLain (1971), homogenized, and analyzed for (Na + K)-ATPase activity by the method of Johnson et al. (1977). All sampled fish were returned alive to the holding tank and were eligible for future sampling. A maximum of four samples were taken per fish. Previous experiments on hatchery-reared coho had determined that the excision of up to three gill tissue samples from an individual fish did not change subsequent gill (Na + K)-ATPase specific activities from that of unclipped control fish.

Once in November and February and twice in March, April, and May, a random sample of 20 juvenile coho was electrofished from upper Knowles Creek. These juveniles were presumed to be nonmigrating fish. Fork lengths and weights were recorded and gill samples were taken for analysis of (Na + K)-ATPase activities from all captured fish. Skins taken from 15 randomly sampled fish on each sample date were analyzed for guanine levels by the method of Staley (1984).

From October through June, migration of juvenile coho from the watershed was monitored by one of two types of downstream migrant trap operated continuously near the mouth of Knowles Creek. At streamflows less than 2.7 m^3/s an inclined plane trap with 6-mm wire mesh wings was used to capture all outmigrating fish. At streamflows equal to or above 2.7 m^3/s a floating scoop trap (Raymond and Collins 1975) was used to capture a proportion of the outmigrants with the total number estimated as described by Rodgers (1986). Scoop trap efficiency varied with streamflow and ranged from approximately 25% at 2.7 m^3/s to 6% at 13.0 m^3/s. Analysis of variance showed no significant monthly differences in streamflow for days that the scoop trap was operated ($F_{7,126} = 1.48$), suggesting that scoop trap efficiency was not biased for a particular time period.

Except during periods of little or no fish movement, migrant traps were checked once in the morning and again at dusk. All captured juvenile coho were enumerated, anesthetized, weighed, and measured. Once in November, December, January, and February and semimonthly thereafter, gill samples for (Na + K)-ATPase activity were collected from the first 20 migrants captured in each of four size groups: (1) <80mm, (2) 80−90 mm, (3) 91−100 mm, and (4) >100 mm. Similarly, skin samples for guanine levels were taken from the first 15 migrants captured in each of the four size groups.

Fork lengths, condition factors, and (Na + K)-ATPase activities of the first 20 migrant coho captured during each sample interval were used for comparison with those of nonmigrants and the captive population. Guanine levels of the first 15 migrant coho captured were used for statistical comparison with those of nonmigrants. Groups were determined to be significantly different from each other if analysis of variance or *t*-tests (Snedecor and Cochran 1980) showed p values ≤0.05. The relationships between skin guanine levels or gill (Na + K)-ATPase activities (Y) and migrant fish fork lengths (X) during any given sample interval were examined using linear regression (Neter and Wasserman 1974). Significance of the correlations was tested under the null hypothesis that slope = 0 using a *t*-test at the 5% level of significance (Snedecor and Cochran 1980).

Results

Approximately 8300 juvenile coho migrated from the Knowles Creek watershed during the study. An early peak in migration occurred during November in conjunction with the first major freshet (Fig. 1). Few fish migrated during low streamflow and water temperature conditions in late December and January. The largest peak in migration occurred during the first 2 wk of May, followed by a gradual decline to near zero during the last 2 wk of June. By this time, few yearling juvenile coho remained in the river system.

Fork lengths of nonmigrant fish were usually smaller and increased more gradually than those of migrants (Fig. 2A). Fish in the captive group of Knowles Creek coho were consistently larger than either migrant or nonmigrant fish, most likely reflecting the effects of warmer rearing water and abundant food under laboratory conditions.

The condition factor of migrant fish reached a maximum in February and then decreased in March (Fig. 2B). Nonmigrant condition factor peaked during the first 2 wk of February and the last 2 wk of April and was significantly higher than either migrants or the captive population of juvenile coho throughout the study. Condition factor of the captive population of juveniles was highest in January and then decreased throughout the remainder of the study.

Skin guanine levels of migrant fish reached minimum levels during March, rose sharply during the first 2 wk of April, and reached a maximum in June (Fig. 3). Skin guanine levels of nonmigrant fish rose during the first of April, decreased by mid-April, and then rose again in May and June to levels not significantly different from those at the first of April. From the last of April until June, guanine levels of nonmigrant fish were less than those of migrant fish. Statistically significant negative correlations existed between the skin guanine levels of migrant fish and their fork lengths in December and February (Table 1),

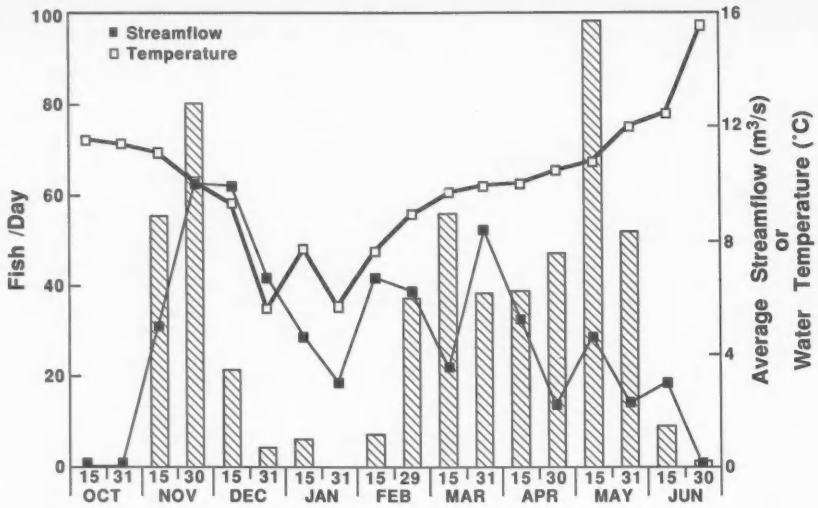

FIG. 1. Average biweekly water temperature, streamflow, and juvenile coho outmigration (vertical bars) from the Knowles Creek watershed.

TABLE 1. Linear correlation between skin guanine level and fork length or gill (Na + K)-ATPase activity and fork length of juvenile coho captured in migrant traps at various time periods in Knowles Creek (*significant at $P \leq 0.05$; **significant at $P \leq 0.01$).

	Skin guanine		Gill (Na + K)-ATPase	
Sample interval	Sample size	Correlation coefficient (r)	Sample size	Correlation coefficient (r)
November	36	−0.334	57	−0.175
December	36	−0.573**	33	−0.303
January	13	−0.350	13	0.346
February	50	−0.320*	68	−0.154
March 1−15	60	0.004	77	−0.068
March 16−31	55	−0.005	56	0.306*
April 1−15	40	0.385*	58	0.229
April 16−30	44	0.017	63	−0.082
May 1−15	34	−0.091	42	0.313*
May 16−31	26	0.107	35	0.232
June	12	0.299	19	0.332

while a positive correlation occurred during the first 2 wk of April and none at any of the other sample intervals.

Average gill (Na + K)-ATPase activity of migrant fish was lowest in January and then rose gradually throughout the remainder of the study (Fig. 2C). Mean gill (Na + K)-ATPase activity of nonmigrants was consistently below that of migrants until the peak of outmigration during the first 2 wk of May when it rose to equal that of migrants (Fig. 2C). Gill (Na + K)-ATPase activity of captive fish peaked during the last 2 wk of April and was not significantly different from nonmigrants until May when it remained below that of either migrants or nonmigrants. Statistically significant positive correlations existed between migrant fish gill (Na + K)-ATPase activities and fork lengths only during the last 2 wk of March and the first 2 wk of May (Table 1).

Discussion

moving to better overwintering habitat in response to changing environmental conditions. Such seasonal changes in behavior have been documented for juvenile coho (e.g. Hartman 1965; Bustard and Narver 1975; Tschaplinski and Hartman 1983).

Smolt indices showed differences between migrant and nonmigrant groups. One of the most common indices of smolting, decreased condition factor, was consistently lower for juvenile coho caught in the migrant traps than for fish electroshocked in the upper watershed. This was probably not due to the stress of capture in the trap, since fish were held in the trap for less than 12 h, a time period insufficient to cause changes in weight of the fish. Thus, decreased condition factor seems to be associated with migration of juvenile coho. The decline in condition factor of the captive group from February through March suggests that these fish would have migrated if given the opportunity.

Increased deposition of guanine in the skin is associated with the silvering that is characteristic of the transition from parr to smolt (Folmar and Dickhoff 1980; Wedemeyer et al. 1980). Increases in skin guanine levels observed in this study were similar to those observed for juvenile Atlantic salmon (*Salmo salar*) (Johnston and Eales 1967) and for coho salmon held in captivity (Staley 1984). In both captive Atlantic and coho salmon, however, guanine in the skin reached a maximum in April and then decreased. This cyclic change was not observed in juvenile coho reared in the wild (Fig. 3).

As outlined in Folmar and Dikhoff (1980) and Wedemeyer et al. (1980), there have been numerous studies linking increases in gill (Na + K)-ATPase activity to the smolting process. In the present study, gill (Na + K)-ATPase activity of migrant juveniles during April was significantly higher than that of nonmigrant fish (Fig. 2C). During the first 2 wk of May, gill (Na + K)-ATPase activity of nonmigrant fish rose to levels similar to migrant fish. These results suggest that migration may be preceded by an increase in gill (Na + K)-ATPase.

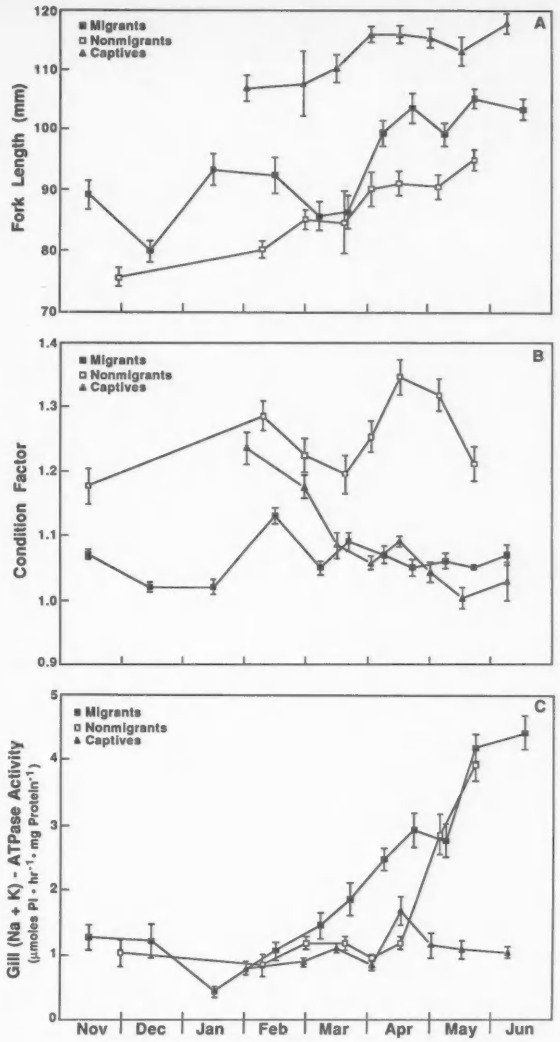

Fig. 2. (A) Fork length, (B) condition factor, and (C) gill (Na + K)-ATPase specific activity of migrant, nonmigrant, and captive groups of juvenile coho sampled from November 1983 to June 1984. All values are means ± SE.

Seaward migration of juvenile anadromous salmonids has traditionally been associated with the transition from parr to smolt. Management agencies have often equated smolts with migrant fish and commonly report all fish captured in migrant traps as smolts. This may be misleading because fish may also migrate for reasons not associated with smolting. Migration of Knowles Creek juvenile coho, as measured by capture in downstream migrant traps, reached two maxima, one in November and one in May. During the first 2 wk of April, fish captured in the traps showed simultaneous increases in gill (Na + K)-ATPase activity, skin guanine, and fork length, a decrease in condition factor, and the first significant elevation of gill (Na + K)-ATPase activity above that of nonmigrants. Because of these physiological changes in the spring and because the seaward migration of coho smolts is generally thought to occur in the spring (Scott and Crossman 1973; Lorz and McPherson 1977), we suggest that the migration of juveniles beginning in April was the result of a smolt migration from Knowles Creek. No such changes were observed during the November peak in migration. This peak in migration was probably the result of juveniles either being displaced by strong stream currents or

Ewing et al. (1979) found a strong positive correlation between the fork length of juvenile spring chinook salmon (*Oncorhynchus tshawytscha*) from the Rouge River and their gill (Na + K)-ATPase activity. Statistically significant relationships were occasionally observed between the size of migrant juvenile coho captured in Knowles Creek and either their gill (Na + K)-ATPase activity or skin guanine levels. However, the low values obtained for correlation coefficients (Table 1) suggest that these relationships are not as well defined in juvenile coho.

Cyclic changes in gill (Na + K)-ATPase activity were not observed in wild coho in the present study. Zaugg (1982) has shown that gill (Na + K)-ATPase activity of hatchery-reared coho peaks and then declines in late April or early May in a pattern similar to that observed for the captive group of juvenile coho in this study. However, in this study, neither migrant or nonmigrant juvenile coho captured in the wild showed any tendency for cyclic changes in gill (Na + K)-ATPase activity. This suggests that the cyclic changes in gill (Na + K)-ATPase activity observed in confined fish may not occur in the wild. In support of this hypothesis, Bjornn et al. (1978), Hart et al. (1981), and Zaugg (1982, 1985) have shown that salmonids released from hatcheries have increased gill (Na + K)-ATPase activity when recaptured downstream.

To insure that the lack of cyclic changes in gill (Na + K)-ATPase activity was not a characteristic of the Knowles Creek stock of coho salmon, individuals were brought to the laboratory in mid-October and adapted to laboratory conditions. Cyclic changes in gill (Na + K)-ATPase activity were observed in these confined fish. Gill (Na + K)-ATPase activity of captive fish reached a maximum in April (Fig. 2C) and decreased in May, but the activity was much lower than in fish captured in the stream. Stress associated with repeated sampling of gills of juveniles was probably not responsible for the slow growth or low activity. Preliminary experiments on coho salmon from Big Creek Hatchery showed that the gills may be clipped as many as three times without affecting either growth or gill (Na + K)-ATPase activity (unpublished data). More likely, confinement and crowding may suppress (Na + K)-ATPase activity (Strange et al. 1978; Hart et al. 1981; Zaugg 1982; Schreck et al. 1985).

In summary, the present study presents insights to problems associated with migration and smolting. Migration can occur with or without changes in physiological factors associated with the parr–smolt transformation. Whether migrations that do not show these changes result in reaching the sea and attaining adulthood remains to be resolved. Changes in physiological factors related to migration may occur at different times. Condition factor was always low in migrants, regardless of month, while gill (Na + K)-ATPase activity of migrants was only higher than that of nonmigrants during March and April. Cylic changes in physiological factors associated with smolting that occur in fish reared in captivity are not evident in juvenile coho reared in the wild. Whether these differences in smolting indices between captive and wild-reared fish result in different survival rates at ocean entry is a matter for future research.

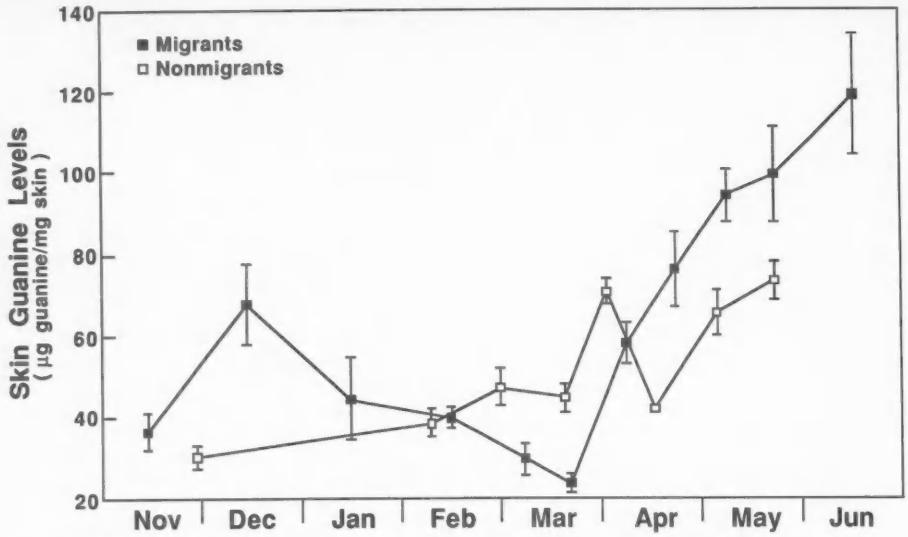

FIG. 3. Skin guanine levels (means ± SE) of migrant and nonmigrant juvenile coho in Knowles Creek, November 1983 to June 1984.

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References

BJORNN, T. C., R. R. RINGE, AND P. HIEBERT. 1978. Seaward migration of Dworshak hatchery steelhead trout in 1976. Univ. Idaho For. Wildl. Range Exp. Stn. Tech. Rep. 6, Moscow, ID. 45 p.

BUSTARD, D. R., AND D. W. NARVER. 1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 32: 667–680.

CEDERHOLM, C. J., AND W. J. SCARLETT. 1981. Seasonal immigrations of juvenile salmonids into four small tributaries of the Clearwater River, Washington, 1977–1981, p. 98–110. *In* E. L. Brannon and E. O. Salo [ed.] Salmon and trout migratory symposium. University of Washington College of Fisheries, Seattle, WA.

CHAPMAN, D. W. 1962. Aggressive behavior in juvenile coho salmon as a cause of emigration. J. Fish. Res. Board Can. 19: 1047–1080.

CHOW, V. T. [ED.] 1964. Handbook of applied hydrology. McGraw-Hill, New York, NY.

EWING, R. D., S. L. JOHNSON, H. J. PRIBBLE, AND J. A. LICHATOWICH. 1979. Temperature and photoperiod effects on gill (Na + K)-ATPase activity in chinook salmon (*Oncorhynchus tshawytscha*). J. Fish. Res. Board Can. 36: 1347–1353.

FOLMAR, L. C., AND W. W. DICKHOFF. 1980. The parr–smolt transformation (smoltification) and seawater adaptations in salmonids. A review of selected literature. Aquaculture 21: 1–37.

HART, C. E., G. CONCANNON, C. A. FUSTISH, AND R. D. EWING. 1981. Seaward migration and gill (Na + K)-ATPase activity of spring chinook salmon in an artificial stream. Trans. Am. Fish. Soc. 110: 44–50.

HARTMAN, G. F. 1965. The role of behavior in the ecology and interaction of underyearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 22: 1035–1081.

HARTMAN, G. F., B. C. ANDERSON, AND J. C. SCRIVENER. 1982. Seaward movement of coho salmon (*Oncorhynchus kisutch*) fry in Carnation Creek, an unstable coastal stream in British Columbia. Can. J. Fish. Aquat. Sci. 39: 588–597.

JOHNSON, S. L., R. D. EWING, AND J. L. LICHATOWICH. 1977. Characterization of gill (Na + K)-activated adenosine triphosphate from chinook salmon, *Oncorhynchus tshawytscha*. J. Exp. Zool. 199: 345–354.

JOHNSTON, C. E., AND J. G. EALES. 1967. Purines in the integument of the Atlantic salmon (*Salmo salar*) during parr–smolt transformation. J. Fish. Res. Board Can. 24: 953–964.

LORZ, H. W., AND B. P. MCPHERSON. 1977. Effects of copper and zinc on smoltification of coho salmon. U.S. Environmental Protection Agency, Ecol. Res. Ser. EPA-600/3-77-032, Corvallis, OR.

MASON, J. C. 1975. Seaward migration of juvenile fishes, including lunar periodicity in the movement of coho salmon (*Oncorhynchus kisutch*) fry. J. Fish. Res. Board Can. 32: 2542–2547.

NETER, J., AND W. WASSERMAN. 1974. Applied linear statistical models. Richard D. Irwin, Incorporated, Homewood, IL.

RAYMOND, H. L., AND G. B. COLLINS. 1975. Techniques for appraisal of migrating juvenile anadromous fish populations in the Columbia River Basin. EIFAC Tech. Pap. 23 (Suppl. 1) 2: 552–565.

RODGERS, J. D. 1986. The winter distribution, movement, and smolt transformation of juvenile coho salmon in an Oregon coastal stream. M.S. thesis, Oregon State University, Corvallis, OR.

SCHRECK, C. B., R. PATINO, C. K. PRING, J. R. WINTON, AND J. E. HOLWAY. 1985. Effects of rearing density on indices of smoltification and performance of coho salmon, *Oncorhynchus kisutch*. Aquaculture 45: 345–358.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.

SNEDECOR, G. W., AND W. G. COCHRAN. 1980. Statistical methods. 7th ed. Iowa State University Press, Ames, IA. 507 p.

STALEY, K. B. 1984. Purine deposition in the skin of juvenile coho salmon (*Oncorhynchus kisutch*). M.S. thesis, Oregon State University, Corvallis, OR.

STRANGE, R. J., C. B. SCHRECK, AND R. D. EWING. 1978. Cortisol concentrations in confined juvenile chinook salmon (*Oncorhynchus tshawytscha*). Trans. Am. Fish. Soc. 107: 812–819.

TSCHAPLINSKI, P. J., AND G. F. HARTMAN. 1983. Winter distribution of juvenile coho salmon (*Oncorhynchus kisutch*) before and after logging in Carnation Creek, British Columbia, and some implications for overwinter survival. Can. J. Fish. Aquat. Sci. 40: 452–461.

WEDEMEYER, G. A., R. L. SAUNDERS, AND W. G. CLARKE, 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. Mar. Fish. Rev. June: 1–14.

ZAUGG, W. S. 1982. Some changes in smoltification and seawater adaptability of salmonids resulting from environmental and other factors. Aquaculture 28: 143–151.

1985. Importance of river migration to the development of seawater tolerance in Columbia River anadromous salmonids. Aquaculture 52: 33–47.

ZAUGG, W. S., AND L. R. MCLAIN. 1971. Gill sampling as a method of following biochemical changes: ATPase activities altered by ouabain injection and saltwater adaptation. Comp. Biochem. Physiol. 38*B*: 501–506.

Energy Reserves of Three Zooplankton Species from Two Lakes with Different Metal Concentrations

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Arts, M. T., and W. G. Sprules. 1987. Energy reserves of three zooplankton species from two lakes with different metal concentrations. Can. J. Fish. Aquat. Sci. 44: 458–466.

Dry weight and lipid content of three zooplankton species in two lakes differing in concentrations of copper, nickel, and aluminum were assayed for two consecutive summers. *Epischura lacustris* and *Holopedium gibberum* had lower lipid levels and were generally lighter in the lake with elevated metals. The lipid droplet in eggs of *H. gibberum* was 21% smaller in the lake with elevated metal levels. Total body burdens of copper in *H. gibberum* were twice as high in the lake with elevated metals. There was no difference in dry weight and levels of energy reserves of *Diaptomus minutus* between the lakes. Lower lipid content and decreased weight of *E. lacustris* and *H. gibberum* from Round Lake could not be explained by lowered food availability, since both the edible portion of phytoplankton biomass and abundance of small *Bosmina* were similar in the two lakes. Since there were no differences in food levels for *E. lacustris* and *H. gibberum* in the two lakes, we attributed lower energy reserves in these species to effects of heavy metal contamination.

Pendant deux étés consécutifs, on a déterminé le poids sec et la teneur en lipides de trois espèces de zooplancton peuplant deux lacs à différentes concentrations de cuivre, de nickel et d'aluminium. Dans le lac à concentration élevée de métaux, *Epischura lacustris* et *Holopedium gibberum* avaient des teneurs en lipides moins élevées et leur poids était en général plus faible. Dans les oeufs de *H. gibberum*, les gouttelettes lipidiques étaient 21 % plus petites dans le cas du lac à concentration élevée de métaux. Les charges corporelles totales de cuivre chez *H. gibberum* étaient deux fois plus élevées dans ce dernier lac. Aucune différence relative au poids sec ou aux niveaux de réserves énergétiques chez *Diaptomus minutus* n'a été relevée d'un lac à l'autre. Une plus faible disponibilité de nourriture n'a pu expliquer la faible teneur en lipides et le poids inférieur de *E. lacustris* et de *H. gibberum* du lac Round car la partie comestible de la biomasse phytoplanctonique et l'abondance de petites *Bosmina* étaient semblables dans les deux lacs. Comme il n'existe aucune différence quant à la quantité de nourriture disponible pour *E. lacustris* et *H. gibberum* d'un lac à l'autre, on attribue les faibles réserves énergétiques chez ces espèces aux effets de la contamination par des métaux lourds.

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Triacylglycerols predominate as an energy reserve in freshwater zooplankton (Goulden and Hornig 1980; Farkas et al. 1981; Goulden and Henry 1984). These energy reserves play a critical role during periods of starvation (Lee and Barnes 1975) and affect competitive ability among neonates (Goulden and Henry 1984). Zooplankton succumb quickly to starvation (Threlkeld 1976); thus, any interference in the accumulation or synthesis of these energy reserves could have important ecological consequences.

Triacylglycerol synthesis may represent a target site for metal cations. Metal ions often exert their toxic effect on aquatic organisms by binding to enzymes and forming transition-metal complexes, with complex stability largely determining the toxicity of the metal ion (Shaw 1961). Effects of metal poisoning on enzyme systems have been documented for sea urchin embryos (Timourian and Watchmaker 1972), crayfish (Hubschman 1967), and fishes (Crandall and Goodnight 1963; McKim et al. 1970; Jackim et al. 1970; Jackim 1973; Bryan 1976). Triacylglycerol synthesis occurs primarily in the cells of the intestinal wall (Goulden and Henry 1984), an important site of uptake for metals such as nickel (Hall 1980). Studies on the ubiquitous fatty acid synthetase complex responsible for the in vivo synthesis of triacylglycerols, in organisms from bacteria to man, have shown that this enzyme can contain up to 90 sulfhydryl groups (Burton et al. 1968, rats and pigeons). Hsu et al. (1965) demonstrated that the enzyme was susceptible to heavy metal inactivation, since chelating agents such as EDTA stimulated activity in the presence of heavy metals as much as 200% over controls without EDTA. Thus, uptake of heavy metals capable of inactivating the fatty acid synthetase complex occurs directly in the intestinal tissue, the major site of triacylglycerol synthesis. The dry weight of some species, for example *Daphnia magna*, is reduced in solutions of copper or nickel (Biesinger and Christensen 1972) and nickel alone (Hall 1980), and since triacylglycerols can contribute significantly to the total dry weight (up to 25% in *Holopedium gibberum*), it seems likely that some of this weight loss could be explained by fat loss. Alternatively, reduction in filtration rates in zooplankton exposed to metals (Flickinger et al. 1982) could result in reduced food gathering ability and thus lower lipid levels.

Numerous estimates of lethal metal concentrations have been made using organisms such as *Daphnia* (Biesenger and Christensen 1972; Baudouin and Scoppa 1974; Winner and Farrell 1976; Shcherban 1977) and trout (Brown and Dalton 1970;

McKim and Benoit 1971; Drummond et al. 1973). While these studies outlined conditions associated with short-term survival, chronic effects of toxins have rarely been assessed (however, see Winner and Farrell 1976; Borgmann et al. 1980), especially under field conditions (Yan and Strus 1980).

We measured triacylglycerol energy reserves (storage fats) in three zooplankton species, *Epischura lacustris* Forbes, *Diaptomus minutus* Lilljeborg, and *Holopedium gibberum* Zaddach, common to a metal-contaminated and an uncontaminated lake in central Ontario. These species occur in 65, 43, and 62%, respectively, of 666 lakes in northeastern North America (Carter et al. 1980). Because of its wide geographical range (Carter et al. 1980) and presence in acid and metal-stressed lakes (Sprules 1975; Yan and Strus 1980), *D. minutus* appears to be a tolerant species. Based on geographical distribution, we predict that if chronic exposure to elevated metal concentration affects triacylglycerols, then *E. lacustris* and *H. gibberum* would have lower levels of triacylglycerols in the metal-contaminated lake whereas *D. minutus* would show little or no difference between the lakes.

Methods

Two lakes were chosen for comparative purposes: Blue Chalk Lake in the Muskoka district of south-central Ontario, which has metal levels at or below the limits of detection of standard atomic absorption methods, and Round Lake, 14 km southwest of Sudbury, Ontario, with substantially higher levels of copper, nickel, and aluminum.

Zooplankton for lipid analyses were obtained at roughly 2-wk intervals, from May to October in 1981 and May to August in 1982, by unmetered vertical townet hauls from bottom to surface at the center of the deepest basin. The large zooplankters *E. lacustris* and *H. gibberum* were collected with a tapered net, length 1.5 m with a 1-m^2 opening, and 1 mm mesh (Nero 1982). This net was used to advantage for *E. lacustris*, since this species can avoid smaller nets and rarely achieves densities in excess of 1.5 animals/L. A Wisconsin-style townet with 30- and 45-cm hoops and 153-μm mesh was used to collect the smaller, more abundant *D. minutus*. Since zooplankton with broken appendages leak significant quantities of storage fat (pers. obs.), both nets were equipped with deep Plexiglas buckets (20 × 7.5 cm) having two small windows (7 × 4 cm of 153-μm mesh) to minimize mechanical damage.

Zooplankton were anaesthesized with carbonated water within 4 h of collection and adults of the three species separated under a dissecting microscope. Cladocerans and copepods were identified using Brandlova et al. (1972) and Smith and Fernando (1978), respectively. The calanoid *E. lacustris* was separated by sex. Only living, intact animals were selected for subsequent analyses, i.e. those that continued twitching under anaesthetic or that had beating hearts. Dead animals, or those with broken appendages, were not used.

After separation, zooplankton were quickly frozen in plastic scintillation vials dipped into a propanol dry-ice bath. The samples were then freeze-dried and stored at −30°C under nitrogen. Prior to lipid extraction, animals were counted and weighed on an electrobalance (Cahn-4401). Between 0.40 and 0.70 mg of *E. lacustris*, 0.16 and 0.22 mg of *D. minutus*, and 0.50 and 1.30 mg of *H. gibberum* tissue (dry weight) were needed to obtain sufficient lipid for reliable measurement. Total fat was extracted by homogenizing samples with 2:1 (v/v) chloroform−methanol in a hand-held glass homogenizer. Centrifugation at 4500 × *g* for 15 min removed heavy carapace components. Triacylglycerols were separated by thin-layer chromatography on silica gel plates (kieselgel 60G, E. Merck Co.). The solvent system used was 90:10:1 (v/v) petroleum ether − diethyl ether − glacial acetic acid (Malins and Mangold 1960). Triacylglycerols were detected with iodine and quantified colorimetrically (Pye Unicam SP6) using a sulfuric acid − dichromate reagent (Armenta 1964). Tripalmitin standard was used for calibration.

The availability of food naturally affects energy reserves in organisms. Therefore, for both lakes, in 1982, we estimated density of *Bosmina longirostris* (O. F. Muller), a small cladoceran that is the major component of the diet of *E. lacustris* (Wong 1981). Roughly every 2 wk, two metered-hauls using the Wisconsin-style townet from bottom to surface over the center of the deepest basin were combined and preserved with 5% formalin. A microcomputer-based measuring device (Sprules et al. 1981) coupled to a dissecting microscope was used to determine densities of *B. longirostris*.

Egg and fat droplet diameters of *H. gibberum* were measured using a dissecting microscope (Wild-Leitz, M5) with an ocular micrometer.

As a rough index of algal food available to the herbivorous *D. minutus* and *H. gibberum*, the biomass of edible algae (<30 μm) was determined in both lakes. Samples were taken with a weighted Tygon tube (6 m × 1 cm) over the deepest basin in the lake at approximately 2-wk intervals in 1981 (May−August). Ten such integrated hauls were combined in a plastic bucket. A 100-mL aliquot was removed for phytoplankton analyses and preserved with Lugol's acidified iodine solution. Five millilitres from this bottle was settled overnight onto a microscope slide that had been pretreated with a gel to enhance adhesion of settled algae (Knoechel and Kalff 1976). Slides were desiccated over silica gel for 24 h. A drop of 10% glycerol in water was added after which slides were preserved by sealing the edges of the coverslip with nailpolish. Counting was done by transects on a binocular, inverted, compound microscope (Leitz Wetzlar, Diavert). Phytoplankton were divided into four groups — unicells, colonies <30 μm in diameter, colonies >30 μm in diameter, and filaments <30 μm — and placed in 1.4-μm size intervals based on cell size (longest dimension). Biovolumes derived from simple geometric models were converted to biomass using a specific gravity of unity. In this way, biomass estimates (wet weight) were made for each size class within a group. Summation of these weights for unicells, colonies, and filaments less than 30 μm was used as an index of edible algal food available.

pH was measured at 2-m intervals from bottom to surface over the center of the deepest basin every 2 wk from May to August in both 1981 and 1982. In 1981, pH was measured with a Hydrolab water monitoring system (Surveyor model 5) whereas in 1982, a portable field meter was used (Corning model 3D).

Water from the consolidated Tygon tube samples was stored in acid-washed 1-L Nalgene bottles for metal analyses. A 100-mL aliquot from these Nalgene bottles was acidified by adding 0.5 mL of nitric acid (BDH-Aristar grade). The aliquot was then evaporated to 5 mL in a 95°C oven. Copper, nickel, and aluminum were measured by inductively coupled plasma atomic emission on a Jobin Yvon-48 spectrophotometer (MOE 1981). Detection limits were 1, 2, and 3 μg/L for copper, nickel, and aluminum, respectively.

All three zooplankton species were segregated in an attempt

TABLE 1. Physical/chemical characteristics of Round Lake and Blue Chalk Lake.

	Round	Blue Chalk
Latitude	46°20′N	45°12′N
Longitude	81°11′W	78°56′W
Elevation (m)	225	335
Surface area (km^2)	5.85	0.35
Max. depth (m)	22	22
Secchi depth (m)	4.8	7.8
pH	6.3–7.1	6.0–7.2
Alkalinity (mg/L as $CaCO_3$)	19.8[a]; 9[b]	6.0
Calcium (mg/L)	8.3[a]; 9.5[b]; 10[c]	3.0; 10[c]
Conductivity (μS/cm)	88[a]; 99[b]; 95[c]	30; 33[c]
Tot. diss. nitrogen (μg/L)	324[a]; 237[b]	261[d]
Tot. diss. phosphorus (μg/L)	6[a]; 7[b]	7.9[d]
Chlorophyll *a* (μg/L)	2.3[a]; 1.1[b]	1.9[d]

[a]Beamish et al. (1975).
[b]Conroy et al. (1978).
[c]This study (1981).
[d]Ontario Ministry of the Environment (1979–80, Dorset Research Centre, P.O. Box 39, Dorset, Ont. P0A 1E0).

to determine total body burden of copper. However, we were only able to collect enough tissue (25 mg) from *H. gibberum*. Copper concentration was determined by flameless atomic absorption spectroscopy (Instrumentation Laboratories, model 351) on acid digests of the freeze-dried tissue using controls in which acid but no tissue was added. Solutions consisting of 10, 30, 50, 100, and 200 μg copper/L were used to derive a standard curve. As a further test, two samples of oyster tissue (National Bureau of Standards, United States of America, certified 63 ± 3.5 μg copper/g tissue) were digested and atomized in the same graphite boats as were used for the *H. gibberum* tissue. Our duplicate copper determinations on oyster tissue yielded a mean value of 74 μg/g and our measurements of copper in *H. gibberum* tissues were corrected accordingly. The average ratio of sample to blank was 8.4 and 4.9 for *H. gibberum* tissue from Round and Blue Chalk Lakes, respectively.

Results and Discussion

There are no consistent differences in pH values between Round Lake and Blue Chalk Lake (Table 1). Alkalinity, calcium, and conductivity were higher in Round Lake, and although *H. gibberum* is usually considered a softwater species, it is not uncommon to find this species in waters with hardness values between 140 and 180 μg/L (Carter et al. 1980). Total dissolved nitrogen and phosphorus as well as chlorophyll *a* were similar (Table 1).

Metal levels in Round Lake are substantially higher than those in Blue Chalk Lake (Table 2). Copper levels similar to those in Round Lake have been considered chronically toxic to fish (Mount and Stephan 1969; McKim and Benoit 1971), snails and amphipods (Arthur and Leonard 1970), and zooplankton (Biesinger and Christensen 1972). Direct comparisons between these studies and Round Lake may not be possible, however, since humic concentrations and water hardness alter toxicity. We cite examples of copper toxicity, since it is difficult to make a strong case for the less toxic nickel (but see Biesinger and Christensen 1972; Timourian and Watchmaker 1972; Pickering 1974; Birge and Black 1980).

TABLE 2. Mean ± SE (sample size in parentheses) summer copper, nickel, and aluminum concentrations (μg/L) in Blue Chalk and Round lakes (1981–82).[a]

Lake	Year	Copper	Nickel	Aluminum
Blue Chalk[b]	1981	3 ± 1.5(3)	2 ± 0.1(3)	13 ± 3.4(4)
	1982	3 (1)	<1 (1)	12 ± 0.01(30)
Round	1981	16 ± 2.4(8)	51 ± 1.5(8)	39 ± 4.7(8)
	1982	22 ± 1.5(6)	55 ± 1.4(6)	46 ± 4.5(6)

[a]Blue Chalk Lake means are from the ice-free period May–November; Round Lake means are from May–August.
[b]Data for Blue Chalk Lake collected by the Ontario Ministry of the Environment, Dorset Research Centre, Dorset, Ont.

Epischura lacustris

Despite the inclusion of between-year variability through pooling data from two summers, our results show that both sexes of *E. lacustris* in Round Lake were generally lighter and had less triacylglycerol (micrograms per animal and micrograms per gram dry weight) than they did in Blue Chalk Lake (Fig. 1 and 2). Slopes of these regression lines are different between the lakes for both sexes (ANCOVA, $p < 0.0005$ and $p < 0.0001$, respectively), suggesting that the net rate of lipid accumulation in *E. lacustris* is less in Round Lake than in Blue Chalk Lake (Table 3). Moreover, the regression lines for both male and female *E. lacustris* from Round Lake (Fig. 1a and 1b) have negative slopes, suggesting that the heaviest animals (generally those in reproductive condition) are most affected in their ability to accumulate triacylglycerol.

Holopedium gibberum

Analyses of the fat versus weight regressions reveal different slopes (ANCOVA, $p < 0.0001$), indicating that the pattern of lipid accumulation differs between the two lakes (Table 3). Triacylglycerol per animal was transformed by taking the $\log_{10}$ to satisfy the underlying assumption of linearity. The slope of the regression line for Round Lake *H. gibberum* is greater than that for Blue Chalk Lake *H. gibberum* (Fig. 3). One interpretation is that in *H. gibberum*, pathways related to somatic growth are more affected by metal exposure than lipid synthesis, forcing animals to mature at a smaller size. Lipid levels in metal-exposed animals, therefore, increase more rapidly with body size than in normal animals; however, the level of total storage fat ultimately attained is much less due to the restriction on body size. In Blue Chalk Lake, lipid reserves increase normally with body size and animal maturity.

Maternal lipid reserves allocated to eggs form a single, large droplet in Cladocera providing a direct assessment of energy available to future neonates and an indirect measure of energy reserves that were diverted to reproduction. In *Daphnia*, roughly 50% of the eggs' energy reserves are utilized during embryonic development (C. Goulden, Division of Limnology and Ecology, Academy of Natural Sciences of Philadelphia, Philadelphia, PA, pers. comm.), the remainder being available to neonates. Thus, triacylglycerol levels in eggs, and eventually in neonates, correlate with survivorship in cohorts and are related to competitive ability (Goulden and Henry 1984). In May 1982, *H. gibberum* from Round Lake had smaller eggs with a reduced lipid volume (Table 4). Because there is little overlap in weight (Fig. 3) and size (Table 4) of *H. gibberum* between the two lakes, we cannot exclude the possibility that

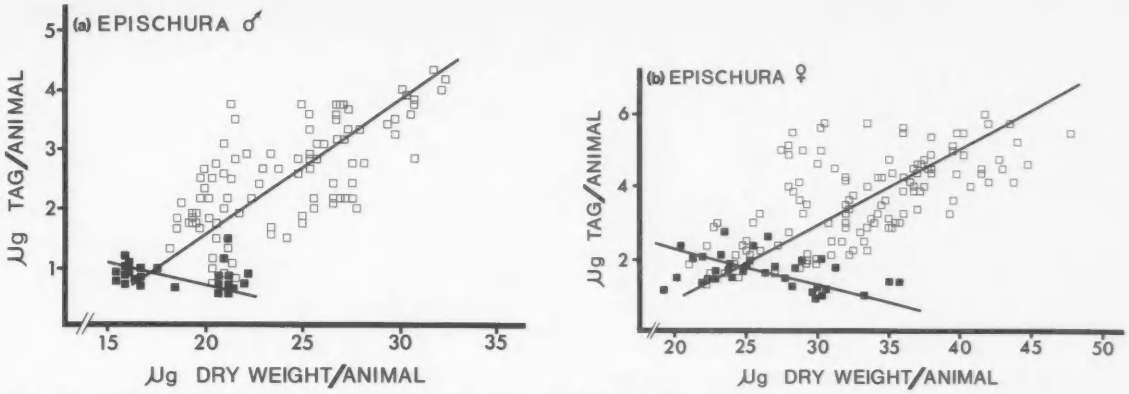

FIG. 1. Triacylglycerol (TAG) levels and dry weights for *E. lacustris* (a) males and (b) females during a 2-yr period from Blue Chalk Lake (open squares) and Round Lake (solid squares). Model II regressions are shown.

TABLE 3. Regression equations (mode I) and analyses of covariance for fat versus weight data presented in Fig. 1, 3, and 5. *Indicates significant differences.

	Blue Chalk		Round			H_0: equal slopes
	Slope	Intercept	Slope	Intercept	F	prob > F
Male *Epischura*	0.16	−1.26	−0.01	1.05	13.01	0.000*
Female *Epischura*	0.13	−0.78	−0.04	2.68	25.62	0.0001*
Holopedium	0.01	−0.41	0.03	−0.90	41.52	0.0001*
Diaptomus	0.65	−0.87	0.76	−1.40	4.22	0.0414*

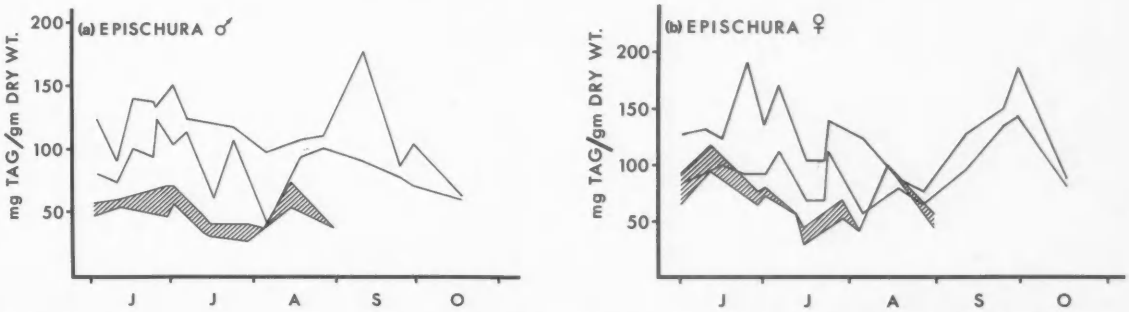

FIG. 2. Seasonal pattern of energy reserves for (a) males and (b) females from Blue Chalk (stippled) and Round (hatched) lakes pooled for two summers. The solid lines are boundaries representing the minimum and maximum TAG levels recorded on each date.

the pattern of lipid allocation for Round Lake *H. gibberum* is part of a normal continuum, reflecting genetic differences between the two populations. It is, however, difficult to conceive of a "natural" selective force that would result in a population composed entirely of individuals with low fat content. Nevertheless, potential for growth during development, and perhaps ultimate size, must surely be affected by lipid stores present during initial, critical periods of development. There remains a possibility, then, that this reduction in energy per egg is related to metal-induced stress and could account for absence of *H. gibberum* neonates in June–July in Round Lake.

In both years, *H. gibberum* from Round Lake persisted only until mid-July and had amassed on the lakes' windward side. Individuals were observed to move only feebly and many were coated with a "surface" growth resembling a fungus. By contrast, Blue Chalk *H. gibberum* persisted until October and ultimately attained levels of storage fats five times greater and body weights three times greater (Fig. 3 and 4) than maximum values recorded for *H. gibberum* from Round Lake. The greater weights attained by Blue Chalk *H. gibberum* are consistent with findings that *D. magna* was lighter after laboratory exposure to acute concentrations of nickel (Hall 1980) and chronic levels of copper or nickel (Biesinger and Christensen 1972).

In 1982, Blue Chalk *H. gibberum* reproduced parthenogenically until October, at which point opaque resting eggs were produced. Throughout summer, females were found carrying eggs with at least three, and occasionally all five,

TABLE 4. Selected reproductive parameters (SE in parentheses) of female *Holopedium gibberum* carrying stage one eggs.[a]

Date	% females with eggs	Mean no. eggs/female	Mean female length (mm)[b]	Egg diam. (μm)	Mean fat diam. (μm)
20 May 1982, Blue Chalk	9.8	9.2 (0.9)	1.4 (0.02)	192.3 (1.5)	83.9 (0.9)
19 May 1982, Round	2.5	3.9 (0.3)	0.8 (0.01)	166.5 (1.4)	77.7 (1.1)

[a]Mean number of eggs/female and mean female length are significantly different between lakes ($p < 0.05$, t-test modified for unequal variances, Sokal and Rohlf, 1981), as are mean fat volumes and egg size ($p < 0.001$, t-test); $n = 50$ in each case.

[b]Segment defined by a point just above the eye, to the most posterior tip of the carapace (refered to as the core body length). These measurements for egg-carrying females only.

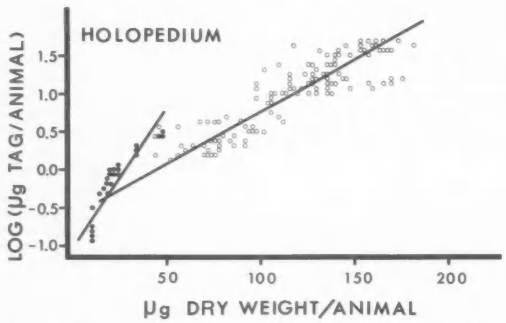

FIG. 3. Log TAG levels and dry weights for *H. gibberum* obtained over a 2-yr period from Blue Chalk Lake (open circles, 23 hidden observations) and Round Lake (solid circles, − 10 hidden observations). Model II regressions are shown.

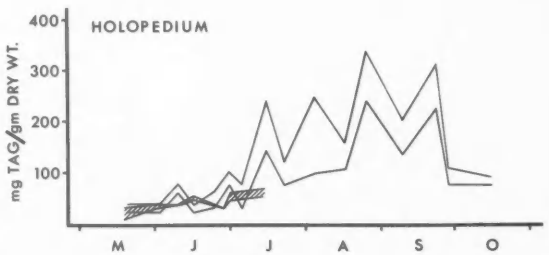

FIG. 4. Seasonal pattern of energy reserves for *H. gibberum* from Blue Chalk (stippled) and Round (hatched) lakes pooled for two summers. The solid lines are boundaries representing the minimum and maximum TAG levels recorded on each date.

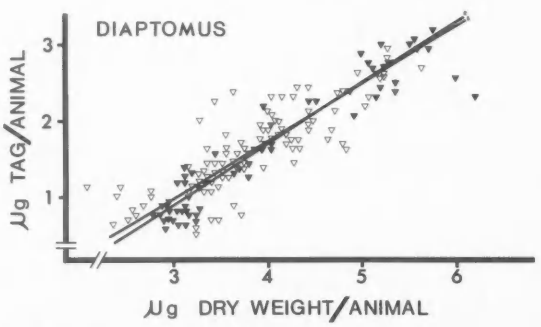

FIG. 5. TAG levels and dry weights for *D. minutus* obtained over a 2-yr period from Blue Chalk Lake (open triangles) and Round Lake (solid triangles). Model II regressions are shown.

developmental stages represented (Threkeld 1979). Round Lake females, by contrast, produced only one parthenogenic summer generation, followed immediately by production of overwintering eggs in June. The summer generation attempt was deemed a failure for three reasons: (1) no females were found in May or June carrying eggs later than stage two; (2) no new neonates were seen entering the population in May−July; and (3) production of resting eggs in June was followed by a sharp population decline to complete disappearance by mid-July. Thus, as opposed to Blue Chalk animals, this population did not persist into the fall to utilize the renewed algal growth stimulated by fall turnover.

Copper levels in tissues of *H. gibberum* from Round Lake were roughly two times greater than those for *H. gibberum* from Blue Chalk Lake (Table 5). Round Lake *H. gibberum* had concentrations of copper that were 1.5−3 times greater than those found in zooplankton of the Sudbury drainage system, undoubtedly reflecting higher levels of copper in waters of Round Lake (Table 5). Although *H. gibberum* from Round Lake experience elevated total body burdens of copper, it does not always follow that there is a positive correlation between body burden and toxic effect of copper (Brown 1977; Dixon and Sprague 1981; Winner 1985).

The observed reproductive impairment (absence of late developmental stages), reduced lipid volume in eggs, the manner of population decline, and elevated copper levels in tissues of *H. gibberum* from Round Lake favor the hypothesis that observed differences in lipid accumulation are due to metal stress. The manner of population deterioration and the small size of *H. gibberum* from Round Lake is reminescent of suggestions of Crandall and Goodnight (1963) and Bryan (1976) that severe inanition produced by metabolic lesions can cause an inhibition of normal growth.

Diaptomus minutus

Contrary to findings for *E. lacustris* and *H. gibberum*, *D. minutus* showed no consistent effects of lake of origin on

TABLE 5. Copper levels in the water (μg/L) and the tissues of zooplankton (μg/g dry weight) taken from various locations. All zooplankton analyzed are mixtures of all species present except for Blue Chalk and Round lakes, which were *H. gibberum* only.

Location	Concn. in water (μg/L)[a]	Concn. in animals (μg/g)	Source
Ontario			
Wanapitei River	7.5	32.5	Hutchinson et al. 1976
Hartley Bay	7.0	36.0	
Western Outlet	5.0	24.0	
Main Outlet	4.0	22.0	
East Outlet	2.0	16.0	
French River	3.0	12.0	
Pickerel River	2.0	15.0	
Blue Chalk Lake	3.0	21.6	This study (1982)
Round Lake	22.0	57.6	This study (1982)
	22.0	48.2	
MELIMEX[b]	4.5–7.0	30–60	Gachter and Geiger 1979

[a]The Sudbury drainage system (Ontario) and Blue Chalk and Round lakes are average summer values.
[b]Estimated from Fig. 1.

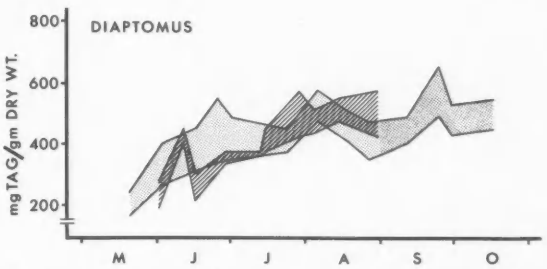

FIG. 6. Seasonal pattern of energy reserves for *D. minutus* from Blue Chalk (stippled) and Round (hatched) lakes pooled for two summers. The solid lines are boundaries representing the mimum and maximum TAG levels recorded on each date.

triacylglycerol content (Fig. 5 and 6). Analyses of covariance on the regressions demonstrated that the differences between the slopes were significant, although not nearly as pronounced as for the former two species (Table 3).

The patterns observed for *E. lacustris* and *H. gibberum* were not seen for *D. minutus* from Round Lake. Rather, the two regression lines broadly overlap and intersect near their midpoints (Fig. 5), suggesting that the slight difference in slope is more the result of normal between-lake variation in lipid storage ability and different sampling times than consistent differences between *D. minutus*' ability to accumulate storage lipids in the two lakes. There was no suggestion of gross perturbation of the reproductive pattern of *D. minutus* in Round Lake, since egg-carrying females were present throughout the season carrying clutches roughly equal in size to late May – early June clutches in Blue Chalk Lake (Table 6). Although gravid females appeared later in Round Lake, they persisted longer, lasting 2 mo compared with only 3 wk in Blue Chalk Lake (Table 6).

Food Densities

Biomass of available food influences the accumulation of energy stores. Grazers readily consume small algae such as

TABLE 6. Mean cephalothorax length and mean number of eggs/female (SE in parentheses) for *D. minutus* from Blue Chalk Lake and Round Lake in 1982. Sample size was 20 in all cases except for Round (2 June) when it was 8.

Lake	Date (1982)	Mean length (mm)[a]	Mean no. eggs/female
Blue	11 May	0.65 (0.0045)	8.7 (0.41)
Chalk	20 May	0.65 (0.0045)	5.3 (0.28)
	28 May	0.67 (0.0067)	3.1 (0.22)
	3 June	0.65 (0.0067)	3.4 (0.20)
Round	2 June	0.76 (0.021)	6.8 (1.1)
	16 June	0.65 (0.0089)	5.3 (0.23)
	1 July	0.63 (0.0045)	3.8 (0.20)
	15 July	0.61 (0.0045)	4.1 (0.14)
	4 August	0.62 (0.0045)	3.5 (0.19)

[a]Length refers to egg-bearing females only.

naked green algae, cryptomonads, nannoflagellates, and certain diatoms, whereas large unicellular algae, colonial forms, or forms possessing a gelatinous sheath remain unaffected when grazing pressure is artificially increased (Porter 1977). Several authors have stressed the importance of nannoplankton as a food source for grazers (Nadin-Hurley and Duncan 1976; Gliwicz 1977; McCauley and Kalff 1981) and specifically those species less than 30 μm (Geller and Muller 1981; Ross and Munawar 1981; Gates et al. 1983; Chow-Fraser 1985).

Biomass of small "edible" phytoplankton (<30 μm) was monitored every 2 wk in 1981 (Fig. 7). Based on a single sample per date, the two lakes do not show large differences in the seasonal pattern of edible algal biomass. This suggests that food availability alone canot account for the lower levels of triacylglycerol found in *E. lacustris* and *Holopedium* in Round Lake. This conclusion is tentative, since we have no data on nannoplankton production rates or the nutritional quality of different species.

Mouthpart morphology (Friedman 1977; C. K. Wong, Institute of Ocean Sciences, Sydney, B.C., pers. comm.) and guts containing both algae and zooplankton indicate that *E. lacustris*

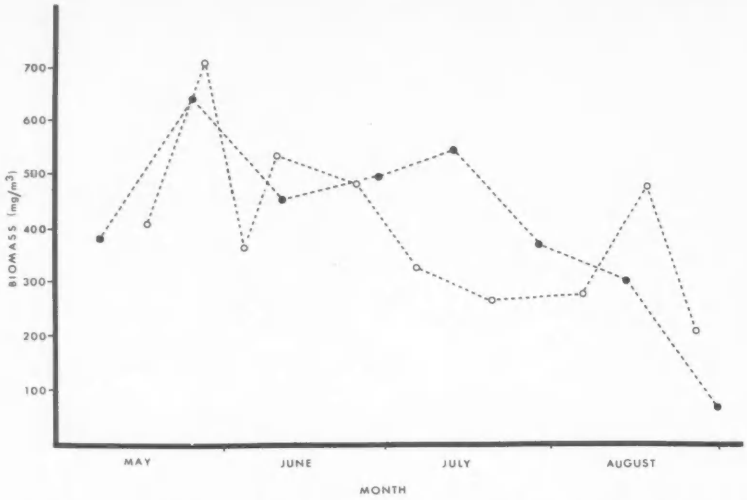

FIG. 7. Biomass of edible algae (<30 μm) in Blue Chalk (open circles) and Round (solid circles) lakes in 1981.

is omnivorous. In laboratory feeding experiments, *E. lacustris* clearly demonstrates a nutritional requirement for invertebrate zooplankton prey (Main 1962) and, in particular, for the cladoceran *B. longirostris* (Wong 1981), selecting this species over other cladocerans such as *Ceriodaphnia* (Wong 1981) and *Daphnia ambigua* (Kerfoot 1977).

The small "feeding basket" formed by mouthparts of *E. lacustris* means that only *B. longirostris* less than 0.40 mm can be effectively handled (Kerfoot 1977; Wong 1981). The continuous availability of *B. longirostris* (<0.40 mm) in Round Lake, at densities matching those in Blue Chalk Lake (Fig. 8), is not surprising, since this zooplankter is encountered frequently in acid- and/or metal-stressed lakes (Haines 1981) and can attain a much greater percentage of total crustacean biomass in acid lakes contaminated with copper and nickel than in comparable low metal, circumneutral lakes (Yan and Strus 1980). Thus, food limitation, in this case *B. longirostris*, does not explain the reduced triacylglycerol levels found in *E. lacustris* from Round Lake when compared with conspecifics from Blue Chalk Lake.

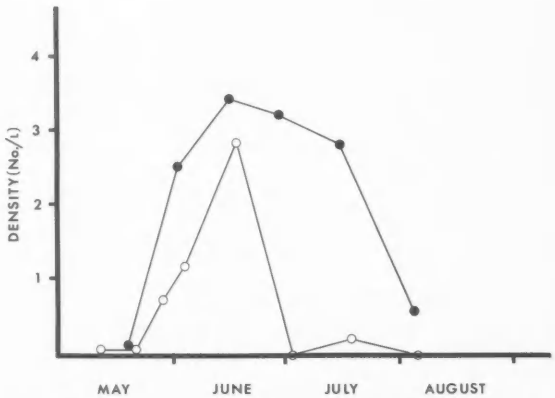

FIG. 8. Seasonal density of *B. longirostris* in Blue Chalk (open circles) and Round (solid circles) lakes in 1982.

Implications

Interference in the accumulation of triacylglycerols would clearly affect the ability of zooplankton to endure periods of food shortage. Loss of certain sensitive species of zooplankton due to heavy metal contamination may result in alterations in the paths of energy flow through trophic levels. The loss of *H. gibberum* and/or *E. lacustris*, when combined with possible losses of sensitive *Daphnia* spp., represents a reduction in the food base for planktivorous fish. This reduction in forage may further aggravate effects of metals in fish, since animals in poor physiological condition succumb to lower levels of metals than "healthy" individuals (Bryan 1976).

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References

ARMENTA, J. S. 1964. A rapid chemical method for quantification of lipids separated by thin-layer chromatography. J. Lipid Res. 5: 270–272.

ARTHUR, T. W., AND E. N. LEONARD. 1970. Effects of copper on *Gammarus psuedolinaeus*, *Physa integra* and *Campeloma decisum* in soft water. J. Fish. Res. Board Can. 27: 1277–1283.

BAUDOUIN, M. F., AND P. SCOPPA. 1974. Acute toxicity of various metals to freshwater zooplankton. Bull. Environ. Contam. Toxicol. 12: 745–751.

BEAMISH, R. J., G. A. MCFARLANE, J. C. VAN LOON, AND J. LICHWA. 1975. An examination of the possible effects of Sudbury nickel mining and smelting operations on fishes and water chemistry of lakes within the Whitefish Lake Indian Reserve. Can. Dep. Environ. Fish. Mar. Serv. Tech. Rep. 579: 52 p.

BIESINGER, K. E., AND G. M. CHRISTENSEN. 1972. Effects of various metals on survival, growth, reproduction and metabolism of *Daphnia magna*. J. Fish. Res. Board Can. 29: 1691–1700.

BIRGE, W. J., AND J. A. BLACK. 1980. Aquatic toxicology of nickel, p. 359–366. *In* J. O. Nriagu [ed.] Nickel in the environment. John Wiley & Sons, Toronto, Ont.

BORGMANN, U., R. COVE, AND C. LOVERIDGE. 1980. Effect of metals on the biomass production kinetics of freshwater copepods. Can. J. Fish. Aquat. Sci. 37: 567–575.

BRANDLOVA, J., Z. BRANDL, AND C. H. FERNANDO. 1972. The Cladocera of Ontario with remarks on some species and distribution. Can. J. Zool. 50: 1373–1403.

BROWN, B. E. 1977. Uptake of copper and lead by a metal-tolerant isopod *Asellus meridianus* Rac. Freshwater Biol. 7: 235–244.

BROWN, V. M., AND R. A. DALTON. 1970. The acute lethal toxicity to rainbow trout of mixtures of copper, phenol, zinc, and nickel, J. Fish Biol. 2: 211–216.

BRYAN, G. W. 1976. Heavy metal contamination in the sea, p. 185–302. *In* R. Johnston [ed.] Marine pollution. Academic Press, New York and London.

BURTON, D. N., A. G. HAAVIK, AND J. W. PORTER. 1968. Comparitive studies of the rat and pigeon liver fatty acid synthetases. Arch. Biochem. Biophys. 126: 141–154.

CARTER, J. C. H., M. J. DADSWELL, J. C. ROFF, AND W. G. SPRULES. 1980. Distribution and zoogeography of planktonic crustaceans and dipterans in glaciated eastern North America. Can. J. Zool. 58: 1355–1387.

CHOW-FRASER, P. 1985. Herbivorous feeding of zooplankton in lakes of south central Ontario. Ph.D. thesis, University of Toronto, Toronto, Ont. 96 p.

CONROY, N., K. HAWLEY, AND W. KELLER. 1978. Extensive monitoring of lakes in the greater Sudbury area, 1974–1976. Water Resources Assessment, North Eastern Region, Ontario Ministry of the Environment.

CRANDALL, C. A., AND C. J. GOODNIGHT. 1963. The effects of sublethal concentrations of several toxicants to the common guppy. Trans. Am. Microsc. Soc. 82: 59–73.

DIXON, D. G., AND J. B. SPRAGUE. 1981. Copper bioaccumulation and hepatoprotein synthesis during acclimation to copper by juvenile rainbow trout. Aquat. Toxicol. 1: 69–81.

DRUMMOND, R. A., W. A. SPOOR, AND G. F. OLSON. 1973. Some short-term indicators of sublethal effects of copper on brook trout, *Salvelinus fontinalis*. J. Fish. Res. Board Can. 30: 698–701.

FARKAS, T., K. KARIKO, AND I. CSENGERI. 1981. Incorporation of [1-^{14}C]acetate into fatty acids of the crustaceans *Daphnia magna* and *Cyclops strenus* in relation to temperature. Lipids 16: 418–422.

FLICKINGER, A. L., R. J. F. BRUINS, R. W. WINNER, AND J. H. SKILLINGS. 1982. Filtration and phototactic behaviour as indices of chronic copper stress in *Daphnia magna* Straus. Arch. Environ. Contam. Toxicol. 11: 457–463.

FRIEDMAN, M. M. 1977. Electron microscope studies of the filter feeding mechanism of calanoid copepods. Ph.D. thesis, Johns Hopkins University, Baltimore, MD. 100 p.

GACHTER, R., AND W. GEIGER. 1979. MELIMEX, an experimental heavy metal pollution study: behaviour of heavy metals in an aquatic food chain. Schweiz. Z. Hydrol. 41: 277–290.

GATES, M. A., A. P. ZIMMERMAN, W. G. SPRULES, AND R. KNOECHEL. 1983. Planktonic biomass trajectories in lake ecosystems. Can. J. Fish. Aquat. Sci. 40: 1752–1760.

GELLER, W., AND H. MULLER. 1981. The filtration apparatus of cladocera: filter mesh-sizes and their implications on food selectivity. Oecologia 49: 316–321.

GLIWICZ, Z. M. 1977. Food size selection and seasonal succession of filter feeding zooplankton in an eutrophic lake. Ekol. Pol. 25: 178–225.

GOULDEN, C. E., AND L. L. HENRY. 1984. Lipid energy reserves and their role in Cladocera. *In* D. G. Meyers and J. R. Strickler [ed.] Trophic interactions within aquatic ecosystems. Am. Assoc. Adv. Sci. Symp. 85: 167–185.

GOULDEN, C. E., AND L. L. HORNIG. 1980. Population oscillations and energy reserves in planktonic Cladocera and their consequences to competition. Proc. Natl. Acad. Sci. USA 77: 1716–1720.

HAINES, T. A. 1981. Acidic precipitation and its consequences for aquatic ecosystems: a review. Trans. Am. Fish. Soc. 110(6): 669–707.

HALL, T. M. 1980. Nickel uptake, retention and loss in *Daphnia magna*. M.Sc. thesis, Department of Botany, University of Toronto, Toronto, Ont. 194 p.

HSU, R. Y., G. WASSON, AND J. W. PORTER. 1965. The purification and properties of the fatty acid synthetase of pigeon liver. J. Biol. Chem. 240: 3736–3746.

HUBSCHMAN, J. H. 1967. Effects of copper on the crayfish *Orconectes rusticus*. Crustaceana 12: 141–150.

HUTCHINSON, T. C., A. FEDORENKO, J. FITCHKO, A. KUJA, J. VAN LOON, AND J. LICHWA. 1976. Movement and compartmentation of nickel and copper in an aquatic ecosystem, p. 568–585. *In* J. O. Nriagu [ed.] Environmental biogeochemistry. Vol 2. Metals, transfer, and ecological mass balances. Ann Arbor Science Publishers, Ann Arbor, MI.

JACKIM, E. 1973. Influence of lead and other metals on fish δ-aminolevulinate dehydrase activity. J. Fish. Res. Board Can. 30: 560–562.

JACKIM, E., J. M. HAMLIN, AND S. SONIS. 1970. Effects of metal poisoning on five liver enzymes in the Killifish (*Fundulus heteroclitus*). J. Fish. Res. Board Can. 27: 383–390.

KERFOOT, W. C. 1977. Implications of copepod predation. Limnol. Oceanogr. 22: 316–324.

KNOECHEL, R. AND J. KALFF. 1976. Track autoradiography: a method for the determination of phytoplankton species productivity. Limnol. Oceanogr. 21: 590–596.

LEE, R. F., AND A. T. BARNES. 1975. Lipids in the mesopelagic copepod, *Gaussia princeps*. Wax ester utilization during starvation. Biochem. Physiol. 52B: 265–268.

MAIN, R. A. 1962. The life history and food relations of *Epischura lacustris*, Forbes (Copepoda:Calanoida). Ph.D. thesis, University of Michigan, Ann Arbor, MI. 135 p.

MALINS, D. C., AND H. K. MANGOLD. 1960. Analysis of complex lipid mixtures by thin layer chromatography and complementary methods. J. Am. Oil Chem. Soc. 37: 576–578.

MCCAULEY, E., AND J. KALFF. 1981. Empirical relationships between phytoplankton and zooplankton biomass in lakes. Can. J. Fish. Aquat. Sci. 38: 458–463.

MCKIM, J. M., G. M. CHRISTENSEN, AND E. P. HUNT. 1970. Changes in the blood of brook trout (*Salvelinus fontinalis*) after short-term and long-term exposure to copper. J. Fish. Res. Board Can. 27: 1883–1889.

MCKIM, J. M., AND D. A. BENOIT. 1971. Effects of long-term exposures to copper on survival, growth, and reproduction of brook trout (*Salvelinus fontinalis*). J. Fish. Res. Board Can. 28: 655–662.

MOE (MINISTRY OF THE ENVIRONMENT). 1981. Outlines of analytical methods. Tech. Rep. MOE, Toronto, Ont. 246 p. plus appendix.

MOUNT, D. I., AND C. E. STEPHAN. 1969. Chronic toxicity of copper to the fathead minnow (*Pimephales promelas*) in soft water. J. Fish. Res. Board Can. 26: 2449–2457.

NADIN-HURLEY, C. M., AND A. DUNCAN. 1976. A comparison of daphnid gut particles with the sestonic particles present in two Thames Valley reservoirs throughout 1970–1971. Freshwater Biol. 6: 109–123.

NERO, R. W. 1982. A description of three nets suitable for estimating the abundance of *Mysis relicta*. Can. Tech. Rep. Fish. Aquat. Sci. 1046: iv + 8 p.

PICKERING, Q. H. 1974. Chronic toxicity of nickel to fathead minnows. J. Water Pollut. Control Fed. 46: 760–764.

PORTER, K. G. 1977. The plant-animal interface in freshwater ecosystems. Am. Sci. 65: 159–170.

ROSS, P. E., AND M. MUNAWAR. 1981. Preference for nannoplankton size fractions in Lake Ontario zooplankton grazing. J. Great Lakes Res. 7: 65–67.

SHAW, W. H. R. 1961. Cation toxicity and the stability of transition-metal complexes. Nature (Lond.) 192: 754–755.

SHCHERBAN, E. P. 1977. Toxicity of some heavy metals for *Daphnia magna* Strauss, as a function of temperature. Hydrobiologia 13: 75–80.

SMITH, K., AND C. H. FERNANDO. 1978. A guide to the freshwater Calanoid and Cyclopoid copepod Crustacea of Ontario. Dep. Biol. Univ. Waterloo. No. 18: 76 p.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. 2nd ed. W. H. Freeman & Co., San Francisco, CA. 411 p.

SPRULES, W. G. 1975. Midsummer crustacean zooplankton communities in acid-stressed lakes. J. Fish. Res. Board Can. 32: 389–395.

SPRULES, W. G., L. B. HOLTBY, AND G. GRIGGS. 1981. A microcomputor-based measuring device for biological research. Can. J. Zool. 59: 1611–1614.

THRELKELD, S. T. 1976. Starvation and the size structure of zooplankton communities. Freshwater Biol. 6: 489–496.

1979. Estimating cladoceran birth rates: the importance of egg mortality and the egg age distribution. Limnol. Oceanogr. 24: 601–612.

TIMOURIAN, H., AND G. WATCHMAKER. 1972. Nickel uptake by sea urchin embryos and their subsequent development. J. Exp. Zool. 182: 379–388.

WINNER, R. W. 1985. Bioaccumulation and toxicity of copper as affected by interactions between humic acid and water hardness. Water Res. 19: 449–455.

WINNER, R. W., AND M. P. FARRELL. 1976. Acute and chronic toxicity of copper to four species of *Daphnia*. J. Fish. Res. Board Can. 33: 1685–1691.

WONG, C. K. 1981. Predatory feeding behaviour of *Epischura lacustris* (Copepoda, Calanoida) and prey defense. Can. J. Fish. Aquat. Sci. 38: 275–279.

YAN, N. D., AND R. STRUS. 1980. Crustacean zooplankton communities of acidic, metal-contaminated lakes near Sudbury, Ontario. Can. J. Fish. Aquat. Sci. 37: 2282–2293.

Evaluating Potential Sources of Mortality for Larval Bloater (*Coregonus hoyi*): Starvation and Vulnerability to Predation

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We evaluated the relative importance of starvation and predation as potential sources of mortality for larval bloater (*Coregonus hoyi*) in the laboratory. Fifty percent of starved bloater larvae survived 25 d after hatching; some individuals survived 35–40 d. Bloater larvae did not exhibit a point of no return, but length and weight after 30 d were inversely related to the delay in first feeding. Bloaters were swimming about half of the time within 1 h after hatching and almost continuously after 6 h. Twenty-one days after hatching, starved larvae were still swimming continuously at 0.9 $cm \cdot s^{-1}$; fed larvae swam more than four times faster. Bloater larvae up to 30 d old were captured with about 80% success by 95- and 135-mm bloaters and 100-mm alewives (*Alosa pseudoharengus*). Susceptibility to predators generally decreased with increasing size, and starved larvae were more susceptible than similar sized fed larvae. Because of their swimming ability and resistance to starvation, it seems unlikely that bloater larvae starve to death in nature. However, starvation can contribute to mortality, as reduced growth and swimming capabilities may result in increased or prolonged susceptibility to predation.

Les auteurs ont évalué l'importance relative de la privation de nourriture et de la prédation comme sources potentielles de mortalité chez les larves de cisco de fumage (*Coregonus hoyi*) gardées en laboratoire. Cinquante pour cent des larves de cisco de fumage affamées ont survécu 25 j après l'éclosion; certains individus ont survécu de 35 à 40 j. Les larves n'ont jamais montré un point de non retour mais après 30 j, le poids et la longueur étaient en relation inverse avec le moment de la première alimentation. Moins de 1 h après l'éclosion, elles nageaient environ la moitié du temps; après 6 h, elles nageaient presque sans interruption. Vingt et un jours après l'éclosion, les larves affamées nageaient encore sans interruption à une vitesse de 0,9 $cm \cdot s^{-1}$ tandis que les larves nourries nageaient à un rythme quatre fois supérieur. Dans 80 % des cas, des ciscos de 95 et 135 mm et des gaspareaux (*Alosa pseudoharengus*) de 100 mm ont capturé des larves de cisco âgées jusqu'à 30 j. En général, la vulnérabilité aux prédateurs a diminué avec l'augmentation de la taille; les larves affamées étaient plus vulnérables que les larves nourries de même taille. À cause de leur capacité natatoire et de leur résistance à la privation de nourriture, il semble peu probable que les larves de cisco de fumage meurent de faim en milieu naturel. Toutefois, la privation de nourriture peut contribuer à la mortalité car des capacités réduites en matière de croissance et de nage peuvent entraîner une vulnérabilité accrue ou prolongée à la prédation.

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Recruitment variability in fishes poses a significant problem for both fisheries ecologists and managers (Steele et al. 1980; Rothschild and Rooth 1982). Causes of recruitment variability are unknown, but hypotheses concerning starvation of larvae (Hjort 1914; Lasker 1975, 1978) and predation or cannibalism on eggs and larvae (Crowder 1980; Hunter and Kimbrell 1980b; MacCall 1981; Hunter 1982) are often suggested to explain "critical periods" in the ontogeny of fishes (May 1974). Here we examine the relative importance of starvation and predation as potential sources of mortality for larvae of the bloater (*Coregonus hoyi*).

The bloater is a native Lake Michigan species and is the only remaining deepwater cisco in the lake after the invasions of exotic rainbow smelt (*Osmerus mordax*), sea lamprey (*Petromyzon marinus*), and alewife (*Alosa pseudoharengus*) (Smith 1970; Wells and MacLain 1973). Bloaters spawn primarily during January through March depositing their eggs on the bottom in deep water, mostly 70–100 m (Wells 1966; Dryer and Beil 1968; Daly et al. 1975; Emery and Brown 1978). The eggs are relatively large, about 2 mm in diameter; larvae are about 9.5–10 mm long at hatching which occurs in late spring and early summer (Wells 1966; Hinrichs 1979; Rice

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1985). Thus, spawning and incubation of the eggs occur under fairly stable physical conditions (cf. Rice 1985). Bloater larvae remain in the hypolimnion for about 10 d after first feeding (Rice et al. 1987) and then migrate to the epilimnion, staying near the surface during the day and moving down as far as the metalimnion at night (Crowder and Crawford 1984).

Although bloaters currently support a commercial harvest of about 1.1 million kg in Wisconsin waters alone, recruitment can be highly variable, recently as much as an order of magnitude among years (E. Brown, Great Lakes Fishery Laboratory, Ann Arbor, MI, pers. comm.). Less than 10 yr ago, bloater populations were so reduced that the fishery was closed lakewide and bloater was placed on the threatened species list in Michigan. Adult bloaters caught in a standard bottom trawl survey were about 450 times more abundant in fall 1984 than in 1977 (Wells and Hatch 1985). Bloater was also historically important as forage for native lake trout (*Salvelinus namaycush*) (Van Oosten and Deason 1938) although little evidence suggests that the current salmonid predator community depends on bloater (Stewart et al. 1981; Hagar 1984).

Bloaters encounter potential predators during both the hypolimnetic and epilimnetic phases of their early life history. While in the hypolimnion, bloater eggs and larvae are sympatric with adult bloater, slimy sculpin (*Cottus cognatus*), and deepwater sculpin (*Myoxocephalus thompsoni*) (Wells 1968), all of which consume bloater eggs and perhaps larvae (Wells and Beeton 1963; Wells 1980; Becker 1983). Because larval bloaters are concentrated in the zone outside the 25-m bottom depth contour, after moving to the surface their most likely predators are pelagic yearling alewife and smelt (Morsell and Norden 1968; Hoagman 1974a; Rhodes et al. 1974; Webb and McComish 1974, O'Gorman 1974; Selgeby et al. 1978).

Mortality due to direct starvation effects depends on food availability and ability of the larvae to resist starvation. Hjort (1914) identified first feeding, when larvae switch from yolk to exogenous feeding, as a critical period of susceptibility. A "point of no return," or time to irreversible starvation, has been identified in many species (May 1974; Hunter and Kimbrell 1980a; Hunter 1981). Among marine fish larvae, resistance to starvation increases with hatching size (Hunter 1981). Once feeding begins, resistance to starvation increases dramatically; energy reserves increase, and as mouth gape and swimming ability increase, a wider range of suitable food sizes becomes available (Blaxter 1969; Hunter 1981).

Susceptibility to predation generally decreases with increasing size and swimming ability (Hunter 1981). As a result, starvation or reduced feeding levels may contribute indirectly to predation mortality by reducing swimming ability and prolonging the time required for larvae to grow through highly susceptible size ranges.

The motivation for exploring causes of bloater recruitment variability rests in the bloater's commercial value, potential importance as food for Lake Michigan salmonids, and the need to understand its potential interactions with the alewife. Our findings also should offer insights into recruitment of other fishes with similar early life histories. In this study, we determine the susceptibility of bloater larvae to direct starvation mortality, test for a point of no return in bloaters, and document the effects of delayed first feeding on their growth, activity level, and swimming speed. The effects of size and starvation on susceptibility of bloater larvae to predation are examined using two potential natural predators, alewife and bloater.

Methods

Bloater eggs were collected in mid-February from adults gill-netted southeast of Milwaukee in Lake Michigan, fertilized in the field, and transported to the Great Lakes Research Facility in Milwaukee, WI. The eggs were incubated in flow-through MacDonald hatching jars until hatching in mid-May. During incubation, temperatures increased with the temperature of Lake Michigan from 3 to 8°C.

In 1983, two groups of newly hatched larvae (425 and 597 individuals) were established in flow-through 5.5-L containers (about 77 and 109 larvae$\cdot L^{-1}$, respectively). Larvae were not fed; dead larvae were collected and counted daily until all had died. In 1984, two larger groups of larvae (963 and 845 individuals) were established in flow-through 95-L tanks (about 10 and 9 larvae$\cdot L^{-1}$, respectively) and treated similarly. Thus, cumulative mortality could be monitored at fish densities differing by an order of magnitude (9−109 fish$\cdot L^{-1}$). Time to 100% mortality was also monitored for a large group of about 20 000 starved larvae held in a 160-L tank. In both years, temperature increased from 8 to 14°C during the experiments. In these and all following experiments a 12L:12D photoperiod was maintained with light levels of >70 lx.

To test bloaters for a point of no return and to examine the effect of delayed first feeding on growth, we held 10 groups of 300 newly hatched larvae in 10 flow-through 4-L containers. Groups were divided into two sets of five tanks; in the first set, one group was starved and the other four groups were fed ad libitum with *Artemia* nauplii twice daily (about 2200 nauplii$\cdot L^{-1}\cdot$feeding^{-1}) starting 4, 8, 12, and 16 d after hatching, respectively; old food was removed periodically. Dead larvae were collected daily to document cumulative mortality for each treatment. The second set was subjected to the same five treatments, but 15 larvae were sampled, without replacements, from each group at 5-d intervals to monitor growth. Fresh total length and dry weight were determined for seven fish and the eight remaining larvae were preserved for otolith analysis (Rice et al. 1985). Both sets of treatments were monitored for 30 d. Temperature increased from 10 to 13.5°C during the experiment, simulating seasonal temperature dynamics in Lake Michigan.

Swimming behavior of unfed larvae was observed at intervals of <1, 6, 12, 18, and 36 h and both starved and fed larvae (first fed 3 d after hatching) were observed at 5, 15, and 21 d after hatching. Larvae were placed in a circular, 22-cm diameter, clear acrylic container containing 4 cm of water, allowed to acclimate about 1 min, and then videotaped for 4 min; observations were made on six individuals for each time interval. For each fish, we recorded the percent time actually swimming. The mean speed while swimming was measured from analysis of the videotape; as the tape was replayed the swimming path of the fish was digitized on the monitor screen with a Grafbar model GP-7 digitizer (Science Accessories Corp.), multiplied by a conversion factor to obtain actual distance travelled in centimetres, and then divided by the time actually swimming. During observations, temperature in the experimental chamber was similar to that in the tank from which the larvae came. Temperatures ranged from 8.5 to 12.3°C but varied <1° during individual trials. Larval behavior and swimming speeds in these trials were consistent with those observed for larvae swimming in 1.25-m-diameter round tanks.

Preliminary predation experiments were conducted using fed

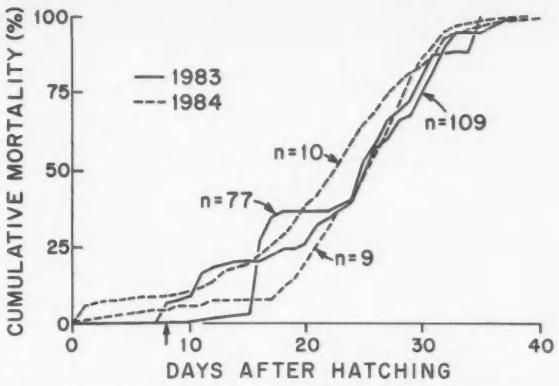

FIG. 1. Cumulative mortality of bloater larvae starved in the laboratory. Water temperatures increased from 8 to 14°C during the experiments. Yolk sac absorption was essentially complete by 8 d after hatching (indicated by arrow on the abscissa). Curve labels indicate initial density of larvae (no. $\cdot L^{-1}$) in each treatment.

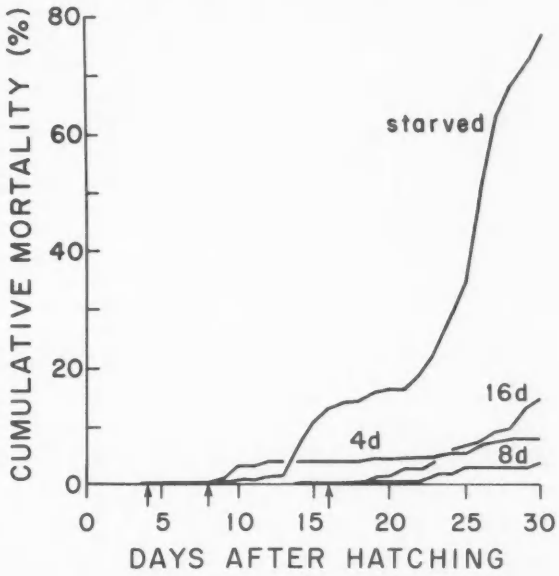

FIG. 2. Cumulative mortality of bloater larvae first fed 4, 8, and 16 d after hatching, or starved. Initial density was 75 fish $\cdot L^{-1}$. The group fed 12 d after hatching was not included in this analysis because 35% of larvae in that group were lost during the experiment, apparently due to a tank overflow. Water temperature increased from 10 to 13.5°C during the experiment. Arrows indicate initial feeding dates.

and starved bloater larvae in a variety of sizes as prey. Alewives (100 mm mean total length) and two sizes of bloaters (95 and 135 mm mean total length) were used as predators. These fish represent potential predators bloater larvae might encounter in the hypolimnetic (bloaters) and epilimnetic (alewives) phases of their ontogeny. Predators were held in 100-L flow-through tanks in groups of three or four. Bloaters were held at 10°C and alewives at 15°C to reflect temperatures commonly occupied in the field (Brandt et al. 1980; Crowder and Magnuson 1982). Several hundred prey were added to the predators' tank and the first 25 attacks were observed. Capture success was determined for each trial, and handling time (time in seconds from prey capture until swallowing) was measured with a stopwatch for some attacks.

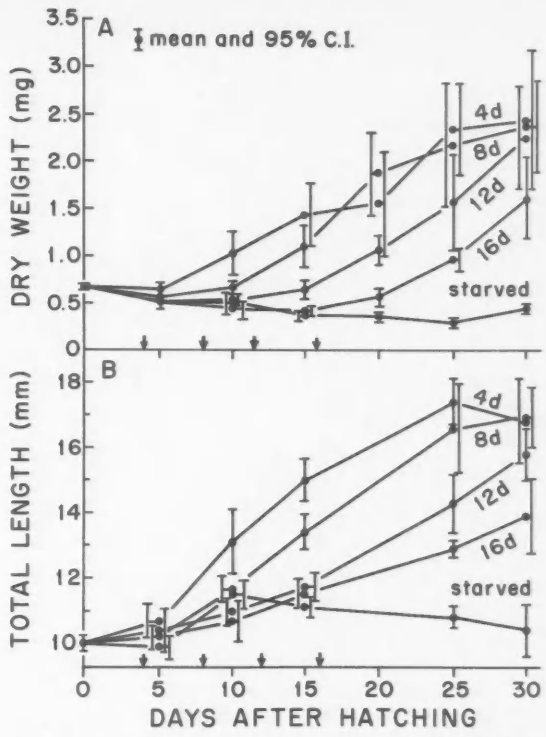

FIG. 3. Growth in (A) dry weight and (B) total length of bloater larvae were fed 4, 8, 12, and 16 d after hatching, or starved. Initial density was 75 fish $\cdot L^{-1}$; $n = 7$ for each point. Water temperature increased from 10 to 13.5°C during the experiment. Arrows indicate initial feeding dates. Total length data from day 20 were lost.

Results

Bloater larvae were very resistant to direct starvation mortality. Fifty percent of bloater larvae survived 25 d after hatching; some individuals survived 35–40 d (Fig. 1). Results did not vary over an order of magnitude of densities; the pattern was similar in all four trials, and in the large group of about 20 000 starved larvae; time to 100% mortality was also 40 d. Yolk sac absorption was essentially complete 8 d after hatching. There was no evidence of a "critical period" at the time of complete yolk absorption. Temperatures during these experiments were somewhat warmer than typical hypolimnion temperatures. Bloater larvae appear to remain in the hypolimnion until 5–10 d after feeding begins (Rice et al. 1987). At cooler temperatures, we expect starved larvae to survive even longer.

Bloater larvae did not exhibit a point of no return even when first feeding was delayed up to 16 d after hatching (8 d beyond yolk sac absorption). Cumulative mortality over the first 16 d of the experiment was low (<5%) for all fed groups, regardless of when feeding began (Fig. 2). Similar low mortality rates were observed for two groups of 1000 larvae each, first fed

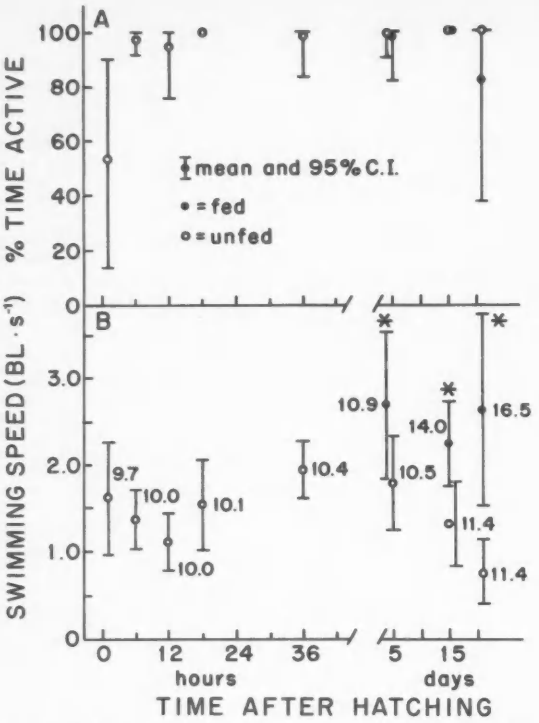

FIG. 4. (A) Activity levels and (B) swimming speeds (excluding periods of inactivity) of fed and starved bloater larvae during 4-min trials. Values near data points indicate mean total length (mm) of larvae in the sample. Asterisks indicate significant differences (*t*-test, $P < 0.05$).

4 d after hatching and reared in 95-L tanks on rations at 600 and 1200 nauplii·L^{-1}·d^{-1}, respectively, in another experiment (Rice et al. 1985). Eighty larvae were sampled from these groups during the first 30 d, but cumulative mortality from other sources was <6% by 16 d and <12% by 30 d in these two groups. When 20 larvae that had been starved for 30 d were offered *Artemia* nauplii, 70% fed within 1 h, suggesting that even beyond 16 d, bloater larvae did not exhibit a distinct point of no return. However, no attempt was made to continue rearing these fish.

While bloaters are not very susceptible to mortality due to direct effects of starvation or delayed first feeding, these treatments strongly reduce size at age (Fig. 3). By 25 d after hatching, larvae first fed on day 4 weighed 2.5 times as much as larvae first fed on day 16. Once feeding began, however, growth rate was similar in fish of similar size. The slight decline in growth rate toward the end of the experiment by the groups fed 4 and 8 d after hatching probably occurred because food levels remained the same, but the larvae were much bigger.

Bloater larvae were strong swimmers; within 1 h after hatching, bloater larvae were swimming about 50% of the time; after 6 h they were swimming almost 100% of the time (Fig. 4A). Even after 21 d of starvation, larvae were still swimming continuously, although more slowly (Fig. 4B). Within 1 h after hatching, larvae were swimming 1.5 body lengths (BL)·s^{-1}. Fed fish were first fed 3 d after hatching, and by 5 d after hatching, swimming speeds of fed bloaters were significantly faster than those of starved bloaters (*t*-test, $P < 0.05$). By 21 d after hatching, fed bloaters were swimming 3.5 times faster than starved larvae in body lengths per second and almost five times as fast in centimetres per second.

Alewife and bloater readily consumed bloater larvae, capturing both fed and starved larvae up to 30 d old with about 80% success (Table 1). Handling times were about 1 s but were too short to measure accurately with a stopwatch over the range of predator and prey types tested. For all three predators, capture success tended to decrease as prey size increased; prey on which capture success was <70% were significantly larger than prey on which capture success was >70% (*t*-test, $P < 0.05$). Capture success by 135-mm bloaters was significantly higher (*t*-test, $P < 0.05$) on starved prey (mean length = 11.0 mm, SD = 0.1, $n = 5$ trials) than on fed prey nearly the same size (mean length = 12.1 mm, SD = 0.3, $n = 7$ trials). It is difficult to separate size and starvation effects because fed larvae are always larger and thus likely to be less vulnerable based on size alone.

Discussion

The strong resistance of bloater larvae to food deprivation may be due primarily to their relatively large size at hatching (9.5 mm total length, 3.25 mg wet weight). Lake herring (*Coregonus artedii*) which hatch at about 12 mm are also resistant to starvation; they show a point of no return at 22 d when reared at about 7°C, but still feed readily after 34 d of starvation at 3–4°C (John and Hasler 1956). Hunter (1981) summarized data on marine fish larvae showing increased resistance to starvation with increased hatching size. Bloaters are twice as resistant to starvation as grunion (*Leuresthes tenuis*) based on days to 50% mortality even though grunion are slightly heavier at hatching. However, grunions also occupy warmer temperatures (20°C). In general, time to point of no return should increase with increasing body size and decrease with increasing temperatures.

Swimming speeds of newly hatched bloater larvae were comparable with those of 10-mm *Coregonus wartmanni* (1.6 cm·s^{-1}, Braum 1967). Bloater swimming speeds clearly increased with body size. In contrast, Hoagman (1974b) found that the swimming speeds of feeding lake whitefish (*Coregonus clupeaformis*) larvae did not increase with size. While starvation had a large effect on swimming speed, bloaters starved 21 d were still swimming continuously at 0.9 cm·s^{-1}. At this rate, even starved larvae would travel almost 33 m and search 10 L water·h^{-1} (assuming a reactive distance of 1 cm, Braum 1967; Hoagman 1974b). Estimated search rates of 21-d starved bloater larvae are comparable with those of feeding *C. clupeaformis* larvae averaging 17 mm (10.8 L·h^{-1}, Hoagman 1974b) and 10-mm *C. wartmanni* (14.6 L·h^{-1}, Braum 1967). In general, volume searched per time tends to be higher for coregonids than for many other fishes (Blaxter 1969). In conjunction with this strong searching ability, newly hatched bloaters have relatively large mouths (mouth gape 0.9 mm, mouth width 0.8 mm, A. Geffen, Center for Limnology, University of Wisconsin, Madison, WI, unpubl. data) and so are not limited to extremely small prey.

Given these attributes, it seems very unlikely that food deprivation would be a major direct source of mortality for bloaters in Lake Michigan. We observed no slow-growing individuals among bloater larvae collected from Lake Michigan in

TABLE 1. Results of predation trials using 95- and 135-mm (TL) bloaters and 100-mm (TL) alewives as predators and fed and starved bloater larvae as prey. Several hundred prey were added and the first 25 attacks observed in each trial. Data were transformed using arcsin $\sqrt{p}$ to calculate confidence intervals.

Predator size (mm TL)	Prey size (mm TL)		Prey age range (d)	Prey fed?	No. of experiments	No. of capture attempts (range)	% successful	
	Mean	Range					Mean	95% C.I.
Bloater (135 mm)	11.0	10.9–11.1	15–20	No	5	16–25	97	91–100
	12.1	11.6–12.5	4–7	Yes	7	18–25	84	76–90
	15.8	15.0–16.5	15–20	Yes	4	25	85	79–91
	21.2	19.5–22	29–41	Yes	3	9–25	83	64–95
Bloater (95 mm)	12.1	11.9–12.5	5–7	Yes	5	20–25	79	72–85
	20.8	19.5–22	29–41	Yes	2	12	55	30–78
Alewife (100 mm)	11.0	10.9–11.1	15–20	No	4	20–25	86	64–99
	15.5	15.0–16.5	15–20	Yes	3	25	69	62–76

1982 and 1983 (Rice et al. 1987); growth rates in the field were generally as high or higher than the highest growth rates observed in the laboratory. Because bloaters do not die quickly when starved, we expected to see at least a few slow-growing individuals in the field if food deprivation were an important factor, but we did not.

Although food deprivation does not appear to be a major direct source of mortality, it may have a large indirect effect on survival, mediated through predation. Starvation reduced the cruising speed of bloater larvae and may have affected their burst speeds as well. Laurence (1972) observed that the maximum speed of largemouth bass (*Micropterus salmoides*) declined with starvation. Susceptibility to predation is frequently influenced by both size and swimming ability (Hunter 1981). Starving or slowly growing larvae may suffer increased predation mortality due to reduced escape ability, or simply because they take longer to grow through size "bottlenecks" of high predation susceptibility (Werner et al. 1983). Regardless, it is clearly beneficial for bloater larvae to feed and grow rapidly to reduce risk of predation.

Some evidence of these starvation and size-related effects can be seen in the preliminary predation trial results reported here, but their influence is probably much more obvious at lower predator/prey size ratios. Even healthy, fast-growing bloater larvae appear very susceptible to both of the potential predators tested, although alternate prey were not offered in these experiments. Bloaters may be more susceptible than other available prey of similar size. When feeding on the largest larvae used as prey in our experiments (22 mm, 35 mg), 100-mm alewives and 95-mm bloaters generally had handling times of <1 s. In contrast, for comparable size *Mysis* (18 mm, 35 mg), handling times would be much higher: 4.6 s for a 100-mm alewife and 5.5 s for a 95-mm bloater (Crowder and Binkowski 1983). Crowder and Binkowski (1983) also reported capture success of a 137-mm bloater feeding on *Mysis* (average size 19.5 mm, 46 mg). Capture seemed to depend on *Mysis* behavior; when *Mysis* moved up off the bottom, capture success was 46 ± 14% (SE), but when they remained on the bottom, capture success was lower, 28 ± 7% (SE). In contrast, capture success of a 135-mm bloater feeding on 19- to 22-mm bloater larvae was 71 ± 9% (SE). These data suggest that bloater larvae not only require a shorter handling time than similar size *Mysis*, but also are easier to capture.

Alewife are known to consume fish larvae in the field (e.g. Wells and Beeton 1963; Wells 1980), but based on published diet data, fish are a minor component of their diet. However, given the abundance of alewives and bloaters, this minor contribution of larvae to total food consumption may be, in fact, a major source of mortality for the larvae. Bloater larvae (14–15 mm) eaten by 100-mm bloaters remained recognizable as bloaters for only 1 h in the gut and as fish larvae for only 2 h (Rice 1985). Any attempt to quantitatively document predation on larvae in the field will require special attention to the constraints imposed by rapid digestion of larvae (cf. Crowder 1980).

Only a minute fraction of bloater larvae survive the first summer of life. Based on our results the predation hypothesis deserves further examination as the major source of mortality. Even for smaller marine fish larvae which one would expect to be more vulnerable to starvation, the hypothesis of a critical period related to first feeding (Hjort 1914; Lasker 1975, 1978) has evolved toward considering multiple mortality bottlenecks (Sharp 1981) and not just starvation at the time of first feeding (Rothschild and Rooth 1982). In particular, support for the hypothesis that predation by both invertebrate and vertebrate predators is important to recruitment variability has been increasing (Hunter 1981; MacCall 1981; Rothschild and Rooth 1982; Hunter 1982; Moller 1984).

In considering predation on larval marine fishes, Hunter (1981, 1982) catalogued a number of potential fish predators for each prey fish species in addition to numerous invertebrate predators from several phyla. In marine systems, invertebrate predation can be a substantial source of larval fish mortality (Theilacker and Lasker 1973; Moller 1984). In Lake Michigan the number of fish predators is limited to just a few species and potential invertebrate predators are limited to several copepods (Hartig et al. 1982) and perhaps *Mysis relicta* (D. Seale, Great Lakes Research Facility, University of Wisconsin-Milwaukee, pers. comm.). The Great Lakes might prove better than marine communities as a model system in which to examine the relation between predation and recruitment variability because the total number and diversity of potential predators is much more constrained.

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References

BECKER, G. C. 1983. Fishes of Wisconsin. University of Wisconsin Press, Madison, WI. 1052 p.

BLAXTER, J. H. S. 1969. Development: eggs and larvae, p. 177–252. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Vol. III. Reproduction and growth. Academic Press, New York, NY, and London, England.

BRANDT, S. B., J. J. MAGNUSON, AND L. B. CROWDER. 1980. Thermal habitat partitioning by fishes in Lake Michigan. Can. J. Fish. Aquat. Sci. 37: 1557–1564.

BRAUM, E. 1967. The survival of fish larvae with reference to their feeding behaviour and the food supply, p. 113–134. *In* S. Gerking [ed.] The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford, England.

CROWDER, L. B. 1980. Alewife, rainbow smelt and native fishes in Lake Michigan: competition or predation? Environ. Biol. Fishes 5: 225–233.

CROWDER, L. B., AND F. P. BINKOWSKI. 1983. Foraging behaviors and the interaction of alewife, *Alosa pseudoharengus*, and bloater, *Coregonus hoyi*. Environ. Biol. Fishes 8: 105–113.

CROWDER, L. B., AND H. L. CRAWFORD. 1984. Ecological shifts in resource use by bloaters in Lake Michigan. Trans. Am. Fish. Soc. 113: 694–700.

CROWDER, L. B., AND J. J. MAGNUSON. 1982. Thermal habitat shifts by fishes at the thermocline in Lake Michigan. Can. J. Fish. Aquat. Sci. 39: 1046–1050.

DALY, R., J. MOORE, AND P. SCHULTZ. 1975. Status of fish stocks, Lake Michigan. Appendix V (b), p. 67–96. Minutes 1975 annual meeting of the Lake Michigan Committee, Great Lakes Fishery Commission, Ann Arbor, MI.

DRYER, W. R., AND J. BEIL. 1968. Growth changes of the bloater (*Coregonus hoyi*) of the Apostle Islands region of Lake Superior. Trans. Am. Fish. Soc. 97: 146–158.

EMERY, L., AND E. H. BROWN, JR. 1978. Fecundity of the bloater (*Coregonus hoyi*) in Lake Michigan. Trans. Am. Fish. Soc. 107: 785–789.

HAGAR, J. M. 1984. Diets of Lake Michigan salmonids: an assessment of the dynamics of predator–prey interaction. Master's thesis, University of Wisconsin, Madison, WI. 87 p.

HARTIG, J. H., D. J. JUDE, AND M. S. EVANS. 1982. Cyclopoid predation on Lake Michigan fish larvae. Can. J. Fish. Aquat. Sci. 39: 1563–1568.

HINRICHS, M. A. 1979. A description and key of the eggs and larvae of five species of fish in the subfamily Coregoninae. Master's thesis, University of Wisconsin, Stevens Point, WI. 73 p.

HJORT, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research: Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 2: 1–228.

HOAGMAN, W. J. 1974a. Feeding by alewives (*Alosa pseudoharengus*) on larval lake whitefish (*Coregonus clupeaformis*) in the laboratory. J. Fish. Res. Board Can. 31: 229–230.

1974b. Vital activity parameters as related to the early life history of larval and postlarval lake whitefish (*Coregonus clupeaformis*), p. 547–558. *In* J. H. S. Blaxter [ed.] The early life history of fish. Springer Verlag, Berlin, Heidelberg, and New York.

HUNTER, J. R. 1981. Feeding ecology and predation of marine fish larvae, p. 33–79. *In* R. Lasker [ed.] Marine fish larvae: morphology, ecology and relation to fisheries. University of Washington Press, Seattle and London.

1982. Predation and recruitment, p. 172–209. *In* B. J. Rothschild and C. G. H. Rooth [ed.] Fish ecology III — a foundation for REX, a recruitment experiment. Univ. Miami Tech. Rep. No. 82008: 389 p.

HUNTER, J. R., AND C. A. KIMBRELL. 1980a. Early life history of pacific mackerel, *Scomber japonicus*. Fish. Bull. 78: 89–101.

1980b. Egg cannibalism in the northern anchovy, *Engraulis mordax*. Fish. Bull. 78: 811–816.

JOHN, K. R., AND A. D. HASLER. 1956. Observations on some factors affecting the hatching of eggs and the survival of young shallow-water cisco, *Leucichthys artedii* LeSueur, in Lake Mendota, Wisconsin. Limnol. Oceanogr. 1: 176–194.

LASKER, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull. 73: 453–462.

1978. The relation between oceanographic conditions and larval anchovy food in the California current: identification of factors contributing to recruitment failure. Rapp. P.-V. Reun. Int. Explor. Mer 173: 212–230.

LAURENCE, G. C. 1972. Comparative swimming abilities of fed and starved larval largemouth bass (*Micropterus salmoides*). J. Fish Biol. 4: 73–78.

MACCALL, A. D. 1981. The consequences of cannibalism in the stock–recruitment relationship. Report and supporting documentation of the workshop on the effects of environmental variation on the survival of larval pelagic fishes, p. 201–220. FAO Intergov. Oceanogr. Comm. Workshop Rep. No. 28.

MAY, R. C. 1974. Larval mortality in marine fishes and the critical period concept, p. 3–19. *In* J. H. S. Baxter [ed.] The early life history of fish. Springer-Verlag, New York, NY.

MOLLER, H. 1984. Reduction of larval herring population by a jellyfish predator. Science (Wash., DC) 224: 621–622.

MORSELL, J. W., AND C. R. NORDEN. 1968. Food habits of the alewife, *Alosa pseudoharengus* (Wilson), in Lake Michigan. Proc. 11th Conf. Great Lakes Res. 1968: 96–102.

O'GORMAN, R. 1974. Predation by rainbow smelt (*Osmerus mordax*) on young-of-the-year alewives (*Alosa pseudoharengus*) in the Great Lakes. Prog. Fish-Cult. 36: 223–224.

RHODES, R. J., D. A. WEBB, AND T. S. MCCOMISH. 1974. Cannibalism by the adult alewife (*Alosa pseudoharengus*) in southern Lake Michigan. Proc. 17th Conf. Great Lakes Res. 1974: 593–595.

RICE, J. A. 1985. Mechanisms that regulate survival of larval bloater *Coregonus hoyi* in Lake Michigan. Ph.D. thesis, University of Wisconsin, Madison, WI. 213 p.

RICE, J. A., L. B. CROWDER, AND F. P. BINKOWSKI. 1985. Evaluating otolith analysis for bloater *Coregonus hoyi*: do otoliths ring true? Trans. Am. Fish. Soc. 114: 532–539.

RICE, J. A., L. B. CROWDER, AND M. HOLEY. 1987. Mechanisms that regulate survival of larval bloater in Lake Michigan: identifying and testing hypotheses using otolith analysis. Trans. Am. Fish. Soc. (In press).

ROTHSCHILD, B. J., AND C. G. H. ROOTH. 1982. Fish ecology III — a foundation for REX, a recruitment experiment. Univ. Miami Tech. Rep. No. 82008: 389 p.

SELGEBY, J. H., W. R. MACCALLUM, AND D. V. SWEDBERG. 1978. Predation by rainbow smelt (*Osmerus mordax*) on lake herring (*Coregonus artedii*) in Western Lake Superior. J. Fish. Res. Board Can. 35: 1457–1463.

SHARP, G. D. 1981. Report of the workshop on effects of environmental variation on survival of larval pelagic fishes, p. 15–64. FAO Intergov. Oceanogr. Comm. Workshop Rep. No. 28.

SMITH, S. H. 1970. Species interactions of alewife in the Great Lakes. Trans. Am. Fish. Soc. 99: 754–765.

STEELE, J., ET AL. 1980. Fisheries ecology: some constraints that impede advances in our understanding. Ocean Sciences Board, National Academy of Sciences, Washington, DC.

STEWART, D. J., J. F. KITCHELL, AND L. B. CROWDER. 1981. Forage fishes and their salmonid predators in Lake Michigan. Trans. Am. Fish. Soc. 110: 751–763.

THEILACKER, G. H., AND R. LASKER. 1973. Laboratory studies of predation by Euphausiid shrimps on fish larvae, p. 287–299. *In* J. H. S. Blaxter [ed.] The early life history of fish. Springer-Verlag, New York, NY.

VAN OOSTEN, J., AND J. DEASON. 1938. The food of the lake trout (*Cristivomer namaycush namaycush*) and of the lawyer (*Lota maculosa*) of Lake Michigan. Trans. Am. Fish. Soc. 67: 157–177.

WEBB, D. A., AND T. S. MCCOMISH. 1974. Food habits of adult alewives in Lake Michigan near Michigan City, Indiana, in 1971 and 1972. Indiana Acad. Sci. 33: 179–184.

WELLS, L. 1966. Seasonal and depth distribution of larval bloaters (*Coregonus hoyi*) in southeastern Lake Michigan. Trans. Am. Fish. Soc. 95: 389–396.

1968. Seasonal depth distribution of fish in southeastern Lake Michigan. Fish. Bull. 67: 1–15.

1980. Food of alewives, yellow perch, spottail shiners, trout-perch, and slimy and fourhorn sculpins in southeastern Lake Michigan. U.S. Fish Wildl. Serv. Tech. Pap. No. 98: 12 p.

WELLS, L., AND A. M. BEETON. 1963. Food of the bloater, *Coregonus hoyi*, in Lake Michigan. Trans. Am. Fish. Soc. 92: 245–255.

WELLS, L., AND R. W. HATCH. 1985. Status of bloater chubs, alewives, smelt, slimy sculpins, deepwater sculpins, and yellow perch in Lake Michigan, 1984. Mimeo report to Great Lakes Fishery Commission Lake Michigan committee, March 19, 1985.

WELLS, L., AND A. L. MACLAIN. 1973. Lake Michigan: man's effect on native fish stocks and other biota. Great Lakes Fish. Comm. Tech. Rep. 20.

WERNER, E. E., J. F. GILLIAM, D. J. HALL, AND G. G. MITTELBACH. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 764: 1540–1548.

NOTES

Nutrient Limitation of Phytoplankton Growth in Brackish Coastal Ponds

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In general, the nutrient most limiting to phytoplankton growth is phosphorus in freshwaters and nitrogen in the sea. We investigated the effect of N and P enrichment to waters from seven brackish, coastal ponds ranging in salinity from 0 to 31 ppt and to nearby coastal seawater (32 ppt). Phytoplankton from the least saline ponds (0–6.5 ppt) responded to P additions, and biomass increased 2–6 times over unenriched controls. Nitrogen additions stimulated phytoplankton growth only in waters from the most saline coastal pond (31 ppt) and seawater. Phytoplankton from ponds of intermediate salinity did not respond when either N or P was added alone but, as in all ponds, increased greatly in biomass when N and P were added in combination. The high salinity at which a switch from P to N limitation occurred could be due to the high N:P loading ratios to these ponds.

En général, les bioéléments qui limitent le plus la croissance du phytoplancton sont le phosphore dans les eaux douces et l'azote dans les eaux salées. Les auteurs ont étudié l'incidence de l'apport de N et de P dans les eaux saumâtres de sept étangs côtiers dont la salinité variait de 0 à 31 ‰ et du milieu marin côtier avoisinant (32 ‰). Le phytoplancton présent dans les étangs moins salés (0–6,5 ‰) a réagi à l'apport de P : la biomasse a augmenté de 2 à 6 fois par rapport aux étangs témoins non enrichis. L'apport d'azote n'a stimulé la croissance du phytoplancton que dans les eaux des étangs côtiers les plus salées (31 ‰) et le milieu marin. Dans les étangs de salinité intermédiaire, le phytoplancton n'a pas réagi aux apports individuels de N ou P mais, comme dans tous les étangs, la biomasse phytoplanctonique a nettement augmenté quand le N et le P ont été ajoutés conjointement. La salinité élevée à laquelle on relève un transfert de la limitation liée à P à une limitation liée à N peut être le résultat des rapports de charge N:P élevés dans le cas de ces étangs.

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The major nutrients limiting phytoplankton growth in aquatic systems are nitrogen and phosphorus (McCarthy 1980; Nalewajko and Lean 1980). In the photic zone of most waters, phytoplankton uptake reduces these elements to very low concentrations. Freshwater and saltwater systems vary, however, in the relative depletion of these two nutrients. The atom ratio of available N:P in freshwater systems is in general greater than the 15:1 ratio required for phytoplankton growth (Schindler 1977). In salt water, the available N:P ratio tends to be equal to or lower than this Redfield ratio (Redfield et al. 1963; Thomas 1966; Nixon 1981; Valiela 1984). The higher N:P ratio in freshwaters indicates that freshwaters are likely to be P limited, and indeed, numerous nutrient addition studies have confirmed this (Vollenweider 1968; Likens 1972; Schindler 1977, 1981; Godfrey 1982; McCoy 1983). In coastal salt waters, on the other hand, N is usually the limiting nutrient (Thomas 1969, 1970; Rhyther and Dunstan 1971; Vince and Valiela 1973). This result is in agreement with the relatively low N:P ratios found in marine systems.

Few studies have been done to determine if there is a fixed point along a salinity gradient where phytoplankton tend to switch from N to P limitation. Thus, it is not known what nutrient is generally limiting in estuaries and coastal ponds which have salinities intermediate between N-limited coastal seawater and those of P-limited freshwater (Schindler 1981). This study determines potential nutrient limitation in a series of eutrophic coastal ponds ranging in salinity from 0 to 31 ppt.

Study Site

The coastal ponds that were used in this study are all located in the town of Falmouth, Massachusetts. They are representative of a large number of coastal ponds located in the glaciated regions of New England. The ponds are located on sandy to cobbly glacial till, and at the time of glaciation were freshwater kettle holes (Emery 1969; Caraco 1986). Due to rise in sea level (Strahler 1966; Emery et al. 1967; Redfield 1967), these ponds presently receive both saltwater and freshwater inputs. Seawater enters these coastal ponds mainly as tidal intrusions through streams adjoining them to Vineyard Sound, while freshwater enters mainly as groundwater seepage (Emery 1969).

The watersheds of the coastal ponds used in our study are densely populated and the ponds receive large amounts of nutrients from septic tank leachate. For example, the loading of N to one of the ponds we studied (Siders Pond) is nearly 3600 $mmol \cdot m^{-2} \cdot y^{-1}$, while P loading is roughly 40 $mmol \cdot m^{-2} \cdot yr^{-1}$ (Caraco 1986). Because of the high nutrient loading, the ponds tend to have relatively high nutrient concentrations as compared with coastal seawater. Dissolved inorganic N concentration in the ponds is about 10–30 μM, with concentrations tending to be highest in the least saline ponds. Phosphate concentrations are also relatively high, averaging 0.1–1 μM during the summer growing season, with concentrations being highest in the most saline coastal pond (Salt Pond) (Emery 1969; Barvenik 1970; Kim and Emery 1971; Caraco 1986).

Methods

Potential nutrient limitation was assayed in batch culture experiments on two dates by adding N and/or P to surface water collected from coastal brackish ponds and nearby seawater. Batch culture assays of nutrient limitation have several problems associated with bottle effects. Despite these problems, these assays yield reliable information on nutrient limitation (McCoy 1983) and seem to be preferable to short-term incubations (Gerhart and Likens 1975). Further, indirect measures of assessing nutrient limitation such as chemistry of suspended particles (Perry 1976) and correlative analysis (Boynton et al. 1980) may be misleading. Results from batch culture nutrient additions are meant here only to show potential nutrient limitation (stimulation of growth with respect to a control) at the time of addition. They are not used to infer what the actual growth rates or standing stock of phytoplankton would be in the field.

The first nutrient enrichment study was begun on 2 July 1982. Water was collected from two coastal ponds (Siders Pond and Salt Pond) and from nearby coastal seawater (Vineyard Sound; Fig. 1). Chlorinity of the water was measured using potentiometric titrations (Cotlove et al. 1958), and salinity was calculated using the relationship of salinity to chlorinity in seawater (Knudsen 1901). The collected water was filtered to remove large zooplankton, and $NaNO_3$ and K_2HPO_4 were added singly or in combination (Table 1). Treatments were done in duplicate. We compared the growth of phytoplankton in these enriched samples with an unenriched control.

TABLE 1. Concentrations of nutrients added during enrichment experiments of July 1982 and October 1982.

	July 1982		October 1982	
Treatment	NO_3 (μM)	PO_4 (μM)	NO_3 (μM)	PO_4 (μM)
Control	0	0	0	0
N	100	0	500	0
P	0	10	0	50
N + P	100	10	500	50

Water was incubated in 8-L jars which were vigorously aerated to prevent settling of phytoplankton. Temperature and illumination were kept constant for the duration of the experiment (~22°C, 45 $\mu Einsteins \cdot m^{-2} \cdot s^{-1}$).

To assess phytoplankton growth, chlorophyll was measured by in vivo fluorescence using a Turner design fluorometer. Measurements were made on days, 3, 5, 9, 12, 15, and 17.

On 13 October 1982, a second nutrient enrichment was started which included five coastal ponds. This experiment was similar to the 2 July 1982 experiment except that NO_3^- and $H_2PO_4^-$ were added at higher concentrations (Table 1). Additionally, incubations were done in small, 50-mL culture tubes rather than in 8-L jars. Fluorescence was measured on days 0, 2, 4, 6, 8, 10, and 12.

Results

Nutrient addition studies — Despite the relatively high nutrient concentrations in the systems studied and the low light levels at which incubations were done, all of the systems at both times of the year were nutrient limited. Peak chlorophyll concentrations reached in N + P additions were in general about 10 times greater than the level in controls (Fig. 1; Fig. 2, top panel). Although the range in response to N + P additions was large (2.5- to 25-fold biomass increase over controls), there was no apparent trend with salinity. In contrast, when either N or P was added alone, phytoplankton response was strongly related to the salinity of the waters (Fig. 1; 2 Fig. 2, center and bottom panels). The phytoplankton from the three least saline systems (Shivericks Pond, 0.1 ppt; Siders Pond (July), 3.5 ppt; Siders Pond (October), 6.5 ppt) were stimulated by P additions (Fig. 2, center panel). Peak biomass reached in the P additions was from 3 to 6 times greater than peak biomass of controls. Nitrogen additions, on the other hand, stimulated phytoplankton growth in only the two most saline systems (Salt Pond (July), 31 ppt; Vineyard Sound, 32 ppt), and in Salt Pond this stimulation was relatively small (twofold the control values). It is interesting that phytoplankton from the ponds of intermediate salinity (Oyster Pond, 6.8 ppt; Trunk River, 8 ppt) and even Salt Pond (Oct.) at 30 ppt responded to neither N nor P additions. In these systems phytoplankton responded only when N and P were added in combination. These ponds, therefore, are borderline between N and P limitation.

Discussion

Despite considerable practical and academic interest, there is

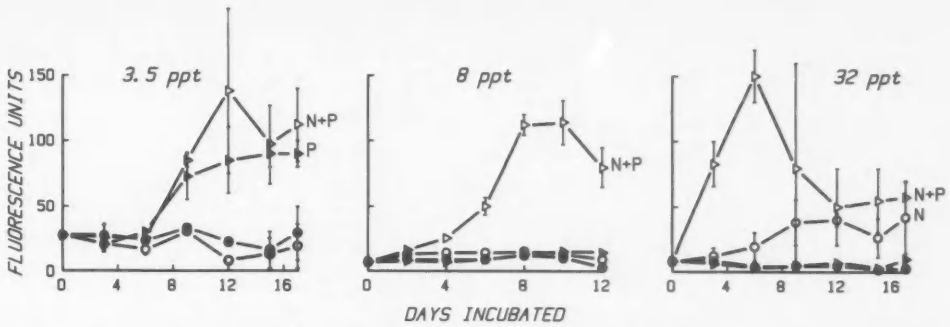

FIG. 1. Representative time-series responses of phytoplankton from coastal ponds and coastal seawater to nutrient enrichments. Left panel, Siders Pond (July addition); center panel, Trunk River (October addition); right panel, Vineyard Sound (July addition). The salinity of each system at the time of nutrient addition is shown.

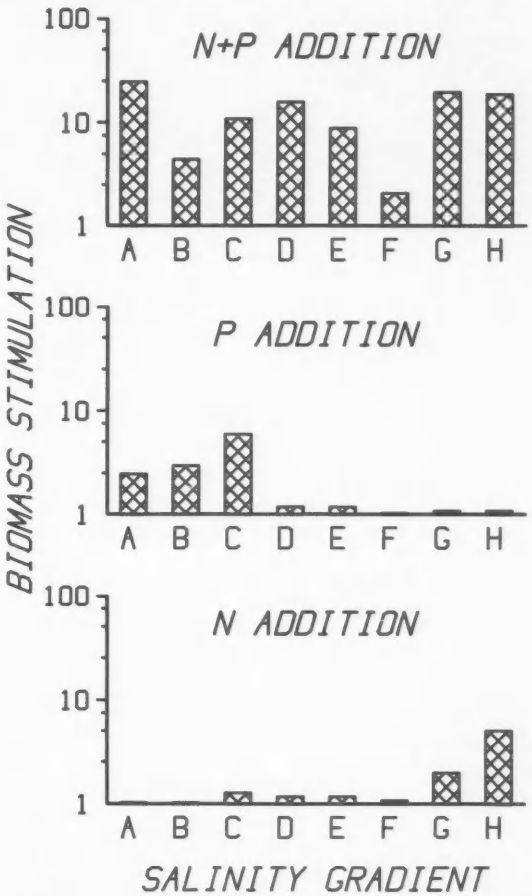

FIG. 2. Stimulation of phytoplankton biomass due to three types of nutrient enrichments made to water from eight systems of varying salinity: A, Shivericks Pond, 0 ppt; B, Siders Pond (July addition), 3.5 ppt; C, Siders Pond (October addition), 6.5 ppt; D, Oyster Pond, 6.8 ppt; E, Trunk River, 8 ppt; F, Salt Pond (October addition), 30 ppt; G, Salt Pond (July addition), 31 ppt; H, Vineyard Sound, 32 ppt. Biomass stimulation (y-axis) is the ratio of peak biomass in the enrichment to that in the unenriched control. Note the log scale.

relatively little data on nutrient limitation of brackish estuaries or coastal ponds. It has been suggested that some brackish systems may not be nutrient limited at all because of the high nutrient loading, short residence time, and high turbidity of these systems (Garside et al. 1976; Schindler 1981). Correlative studies and some nutrient enrichment studies suggest, however, that nutrient loading (or concentration) is an important variable determining phytoplankton productivity in brackish systems (Ketchum 1969; Norin 1977; Boynton et al. 1980). In agreement with these studies, our data, based on nutrient enrichments, demonstrated that in several brackish coastal ponds, P and N were important variables determining phytoplankton growth. The addition of these two nutrients to the water from coastal ponds ranging in salinity from 0 to 31 ppt resulted in significant increases in phytoplankton biomass (Fig. 2). Thus, there is evidence that, like freshwater and coastal seawater, primary production in brackish waters is, in general, nutrient limited and N and P are important limiting nutrients.

In addition to determining if nutrients were limiting to phytoplankton growth in brackish systems, we wished to determine if there was a switch from P to N limitation along a salinity gradient. This salinity related switch might be expected, as freshwaters tend to be P limited, while coastal seawater is N limited (Smith 1984; Howarth and Cole 1985). We know of only one other study that looked at nutrient limitation along a salt gradient (Norin 1977). This study of nutrient limitation in the Baltic suggested that a switch from P to N limitation did, in fact, occur. In waters under about 2 ppt the phytoplankton were P limited, while in saltier waters, phytoplankton were N limited. In agreement with this, we demonstrated a switch from P to N limitation with increasing salinity in a series of coastal ponds. Our results differed from those of Norin (1977), however, in that ponds were P limited from 0 to 6.5 ppt and only the most saline pond (31 ppt) showed N limitation. Thus, in the ponds we studied, P was relatively more important in controlling plankton growth than in the Baltic Sea. This difference could be due to the difference in N:P loading ratios between these sites. In agreement with this, data suggest that N:P loading ratios for these coastal ponds may be as high as 90:1 (Caraco 1986), while in the Baltic this loading ratio is near 30:1 (Sen Gupta 1973). Analysis of N:P loading ratios and nutrient limitation in various estuaries and coastal ponds would help determine if nutrient limitation in most brackish waters is, in fact, controlled primarily by external loading ratios.

References

BARVENIK, F. W. 1970. The microbial ecology of sulfur transformations in Oyster Pond, Woods Hole, Massachussetts. Ph.D. thesis, University of New Hampshire, Durham, NH. 341 p.

BOYNTON, W. B., W. M. KEMP, AND C. W. KEEFE. 1980. A comparitive analysis of nutrients and other factors influencing estuarine phytoplankton production, p. 69–90. *In* V. S. Kennedy [ed.] Estuarine perspectives. Academic Press, New York, NY.

CARACO, N. 1986. Phosphorus, iron, and carbon cycling in a salt stratified coastal pond. Ph.D. thesis, Boston University, Boston, MA. 213 p.

COTLOVE, E., H. V. TRANTHAN, AND R. L. BOWMAN. 1958. An instrument for automatic, rapid, accurate, and sensitive titration of chloride in biological samples. J. Lab. Clin. Med. 51: 461–468.

EMERY, K. O. 1969. A coastal pond studied by oceanographic methods. American Elsevier, New York, NY.

EMERY, K. O., R. L. WIGLEY, A. S. BARTLETT, M. RUBING, AND E. S. BARGHOORN. 1967. Freshwater peat on the continental shelf. Science (Wash., DC) 158: 1301–1307.

GARSIDE, C., T. C. MALONE, O. A. ROELS, AND B. A. SHARFSTEIN. 1976. An evaluation of sewage derived nutrients and their influence on the Hudson River Estuary and New York Bight. Estuarine Coastal Mar. Sci. 4: 281–299.

GERHART, D. Z., AND G. E. LIKENS. 1975. Enrichment experiments for determining nutrient limitation: four methods compared. Limnol. Oceanogr. 20: 649–653.

GODFREY, P. J. 1982. The eutrophication of Cayuga Lake: a historical analysis of the phytoplankton response to phosphate detergent. 17: 149–166.

HOWARTH, R. W., AND J. J. COLE. 1985. Molybdenum availability in natural waters. Science (Wash., DC) 229: 653–655.

KETCHUM, B. H. 1969. Eutrophication of estuaries, p. 197–221. *In* G. A. Rohlich [ed.] Eutrophication: causes, consequences, correctives. National Academy of Sciences, Washington, DC.

KIM, C. M., AND K. O. EMERY. 1971. Salt Pond topography, sediments, and water. Salt Pond Area Bird Sanctuaries, Inc. Annual Rep.

KNUDSEN, M. 1901. Hydrographical tables. According to the measurings of Carl Fosch, P. Jacobsen, Martin Knudsen, and S. P. L. Sorensen, G. E. C. Gad, Williams, Copenhagen.

LIKENS, G. E. [ED.] 1972. Eutrophication and aquatic ecosystems. American Society of Limnology and Oceanography, Lawrence, KS.

MCCARTHY, J. J. 1980. Nitrogen, p. 199–233. *In* I. Morris [ed.] The physiological ecology of phytoplankton. University of California Press, Berkeley, CA.

MCCOY, G. A. 1983. Nutrient limitation in two arctic lakes, Alaska. Can. J. Fish. Aquat. Sci. 40: 1195–1202.

NALEWAJKO, C., AND D. R. S. LEAN. 1980. Phosphorus, p. 235–258. *In* I. Morris [ed.] The physiological ecology of phytoplankton. University of California Press, Berkeley, CA.

NIXON, S. W. 1981. Remineralization and nutrient cycling in coastal marine ecosystems, p. 111–138. *In* B. J. Neilson and E. Cronin [ed.] Estuaries and nutrients. Humana Press.

NORIN, L. L. 1977. ^{14}C-bioassays with the natural phytoplankton in the Stockholm archipelago. Ambio Spec. Rep. 5: 15–21.

PERRY, M. J. 1976. Phosphate utilization by an oceanic diatom in phosphorus-limited chemostat culture and in the oligotrophic waters of the central north Pacific. Limnol. Oceanogr. 21: 88–103.

REDFIELD, A. C. 1967. Postglacial change in sea level in the western north Atlantic. Science (Wash., DC) 157: 687–691.

REDFIELD, A. C., B. H. KETCHUM, AND F. A. RICHARDS. 1963. The influence of organisms on the composition of seawater, p. 26–77. *In* M. N. Hill [ed.] The sea. Vol. 2. Interscience, New York, NY.

RHYTHER, J. H., AND W. M. DUNSTAN. 1971. Nitrogen, phosphorus, and eutrophication in coastal marine environments. Science (Wash., DC) 171: 1008–1013.

SCHINDLER, D. W. 1977. Evolution of phosphorus limitation in lakes. Science (Wash., DC) 195: 260–262.

1981. Studies of eutrophication in lakes and their relevance to the estuarine environment. *In* B. J. Nielson and L. E. Cronin [ed.] Estuaries and nutrients. Humana Press.

SEN GUPTA, R. 1973. A study on nitrogen and phosphorus and their interrelationships in the Baltic. University of Gothenburg, Institute of Oceanography, Gothenburg, Sweden.

SMITH, S. V. 1984. Phosphorus versus nitrogen limitation in the marine environment. Limnol. Oceanogr. 29: 1149–1160.

STRAHLER, A. N. 1966. A geologist's view of Cape Cod. Natural History Press, New York, NY.

THOMAS, W. H. 1966. Surface nitrogenous nutrients and phytoplankton in the northeastern tropical Pacific Ocean. Limnol. Oceanogr. 11: 293–400.

1969. Phytoplankton nutrient enrichment experiments off Baja California and in the eastern equatorial Pacific Ocean. J. Fish. Res. Board Can. 26: 1133–1145.

1970. Effect of ammonium and nitrate concentration on chlorophyll increases in natural tropical Pacific phytoplankton populations. Limnol. Oceanogr. 15: 386–394.

VALIELA, I. 1984. Marine ecological processes. Springer-Verlag, New York, NY.

VINCE, S., AND I. VALIELA. 1973. The effects of ammonium and phosphate enrichments on chlorophyll a, pigment ratios, and species composition of phytoplankton of Vineyard Sound. Mar. Biol. 19: 69–73.

VOLLENWEIDER, R. A. 1968. Scientific fundamentals of eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. OECD Tech. Rep. DAS/C51/68.27. Paris, France.

Lentic Spawning by the Pacific Lamprey, *Lampetra tridentata*

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Anadromous Pacific lamprey, *Lampetra tridentata*, typically construct nests and reproduce in lotic environments. In the summer of 1984, Pacific lamprey were observed spawning in shallow lentic water in two regions of the Babine Lake system, British Columbia. Nests were subject to wave action but an obvious unidirectional flow was not observed.

La lamproie du Pacifique anadrome, *Lampetra tridentata*, construit généralement un nid et se reproduit en milieu lotique. À l'été 1984, on a observé des lamproies du Pacifique frayant en milieu lentique peu profond dans deux régions du système du lac Babine (Colombie-Britannique). Les nids étaient soumis à l'action des vagues quoiqu'un courant unidirectionnel n'ait pas été observé.

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Generally, lampreys spawn in the shallow regions of streams, in moderate to swift current on sand and gravel substrates (Applegate 1950). A unidirectional current is thought to be a requirement for spawning (Applegate 1950; Hardisty and Potter 1971; Manion and Hanson 1980). Lamprey larvae are customarily found in the sandy silt substrate of their natal streams and occasionally, they are found in the substrate of estuaries or nearby bays (Thomas 1961; Wagner and Stauffer 1962a, 1962b; Dodge 1965; Potter 1980; Farlinger and Beamish 1984). The presence of sea lamprey, *Petromyzon marinus*, larvae in lentic environments is attributed to downstream migration or drift (Wagner and Stauffer 1962a, 1962b; Manion and McLain 1971). This study describes observations on spawning by Pacific lamprey, *Lampetra tridentata*, in the lentic waters of the Babine Lake system, British Columbia.

Study Area

Babine Lake, Babine River, and Nilkitkwa Lake are part of the Babine Lake system in north-central British Columbia (Farlinger and Beamish 1984). Babine Lake is 150 km long, has a mean depth of 55 m, and a surface area of 491 km^2 (Johnson 1965). Many small rivers discharge into Babine Lake. Outflow by way of the Upper Babine River is to the north. An enlargement of the Babine River, known as Nilkitkwa Lake, separates the Upper and Lower Babine rivers. The Lower Babine River flows to the Skeena River and ultimately to the Pacific Ocean.

Results and Discussion

Anadromous Pacific lamprey have long used the lower tributaries of the Skeena River for reproduction and larval development (Pletcher 1963; Farlinger and Beamish 1984). Recently, Pacific lamprey have extended their range by colonizing Babine Lake and a number of its tributaries (Farlinger and Beamish 1984). Spawning occurs between early June and late July in the Babine River and several of the small tributaries that discharge into Babine and Nilkitkwa lakes. On July 9, 1984, one pair of Pacific lamprey was observed spawning on a gravel bar 30 m from the mouth of Nine-Mile Creek, a small tributary to the north arm of Babine Lake. Depth at the spawning site was about 50 cm. Buoys placed in the water over the nest appeared to be directed primarily by wave action. Further, bottom sand, when disturbed, failed to reveal a current. The spawning pair were, however, loosely oriented towards the mouth of the creek, suggesting that they were in some way cued to the stream. On August 5, 1984, after all lamprey spawning was completed, five nests were counted, suggesting that more than one pair of lamprey spawned on this gravel bar.

On June 28, 1984, several pairs of lampreys were observed spawning on gravel bars 2–3 m in depth at the lower end of Nilkitkwa Lake. Nine nests were counted. Again no flow was evident.

Spawning behavior in lentic spawning locations was similar to that observed in tributary streams and was consistent with descriptions provided for Pacific lamprey by Pletcher (1963). Males attached to the head of females and twisted tightly around females as both arched their bodies and undulated violently. Eggs were deposited in bowl-shaped nests, 20–30 cm in diameter, 4–8 cm in depth and constructed in gravel ranging from 1 to 8 cm in diameter. Egg development and hatching success were not monitored.

The frequency of lentic relative to lotic spawning in the Babine system is low. A total of 14 nests was counted in lentic environments in this study in comparison with the 1442 nests identified earlier in lotic water in the Babine system by Farlinger and Beamish (1984).

Lampreys prefer a unidirectional flow and generally do not spawn in lakes. Applegate (1950) reported that sea lamprey did not spawn in currents less than 40 $cm \cdot s^{-1}$, while Manion and Hanson (1980) noted that a unidirectional flow of between 50 and 150 $cm \cdot s^{-1}$ was preferred. Hardisty and Potter (1971) observed that European brook lamprey, *Lampetra planeri*, spawn in currents of 30–50 $cm \cdot s^{-1}$. Farlinger and Beamish (1974) reported Pacific lampreys spawning in areas of Babine Lake with a definite and consistent unidirectional flow. In laboratory spawning studies, *L. tridentata* spawned only when a strong unidirectional current was present (R. J. Beamish, unpubl. data). In contrast, our observations suggest that a unidirectional flow may not always be a requirement for the Pacific lamprey.

Spawning in the absence of a unidirectional current has been observed for few lamprey species. Scott (1957) reported that one pair of sea lamprey spawned successfully in a still-water enclosure in the Root River (Lake Huron). Recent field observations indicate that lentic spawning occurs sometimes in *Lampetra richardsoni* (R. J. Beamish, unpubl. data). In the laboratory, both *L. richardsoni* (Pletcher 1963; Richards et al. 1982; R. J. Beamish, unpubl. data) and *Lampetra ayresi* (Richards et al. 1982; R. J. Beamish, unpubl. data) have reproduced successfully in still-water tanks.

Lentic spawning has also been reported for *Lampetra macrostoma* (Beamish 1982) and the now extinct *Lampetra minima* (Bond and Kan 1973; Kan and Bond 1981). This is particularly interesting in view of the present observations, since *L. macrostoma* and *L. minima* are believed to be recent derivatives of *L. tridentata* and to have developed a lake spawning behavior in association with their evolution to a freshwater parasitic life history type (Bond and Kan 1973; Kan and Bond 1981; Beamish 1982).

The implications of lentic spawning in lamprey are important where control of their numbers is practised. Control of sea lamprey abundance in the Great Lakes is directed at the removal of stream-dwelling larvae through chemical treatment (Smith and Tibbles 1980). Lamprey larvae in lentic environments complicate control efforts, since no effective meth-

odology exists for the removal of larvae in lentic areas within the Great Lakes. Although the majority of lake-dwelling larvae are likely due to downstream drift, this study suggests that lentic spawning may also occur. It is conceivable that chemical control of larvae in rivers may favor selection for lentic spawning.

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References

APPLEGATE, V. C. 1950. Natural history of the sea lamprey (*Petromyzon marinus*) in Michigan. U.S. Dep. Inter. F.W.S. Spec. Sci. Rep. Fish 55: 237 p.

BEAMISH, R. J. 1982. *Lampetra macrostoma*, a new species of freshwater parasitic lamprey from the west coast of Canada. Can. J. Fish. Aquat. Sci. 39: 736–747.

BOND, C. E., AND T. T. KAN. 1973. *Lampetra (Entosphenous) minima* n. sp., a dwarfed parasitic lamprey from Oregon. Copeia: 568–574.

DODGE, D. . 1965. Estimates of population densities of sea lamprey ammocoetes in certain bays of Lake Superior, 1964. Fish. Res. Board Can. Biol. Stn. Lond. Annu. Rep. 1964–1965. Append. 37.

FARLINGER, S. P., AND R. J. BEAMISH. 1984. Recent colonization of a major salmon-producing lake in British Columbia by the Pacific lamprey (*Lampetra tridentata*). Can. J. Fish. Aquat. Sci. 41: 278–285.

HARDISTY, M. W., AND I. C. POTTER. 1971. The general biology of adult lampreys, p. 127–206. *In* M. W. Hardisty and I. C. Potter [ed.] The biology of lampreys. Vol. 1. Academic Press, London.

JOHNSON, W. E. 1965. The morphometry of Babine Lake and Nilkitkwa Lake. Fish. Res. Board Can. MS Rep. 819: 16 p.

KAN, T. T., AND C. E. BOND. 1981. Notes on the biology of the Miller Lake lamprey *Lampetra (Entosphenus) minima*. Northwest Sci. 55: 70–74.

MANION, P. J., AND L. H. HANSON. 1980. Spawning behavior and fecundity of lampreys from the upper three Great Lakes. Can. J. Fish. Aquat. Sci. 37: 1635–1640.

MANION, P. J., AND A. L. MCLAIN. 1971. Biology of larval sea lampreys (*Petromyzon marinus*) of the 1960 year-class, isolated in the Big Garlic River, Michigan, 1960–65. Great Lakes Fish. Comm. Tech. Rep. 16: 35 p.

PLETCHER, F. T. 1963. The life history and distribution of lampreys in the Salmon and certain other rivers in British Columbia, Canada. M.Sc. thesis, University of British Columbia, Vancouver, B.C. 195 p.

POTTER, I. C. 1980. Ecology of larval and metamorphosing lampreys. Can. J. Fish. Aquat. Sci. 37: 1641–1657.

RICHARDS, J. E., R. J. BEAMISH, AND F. W. H. BEAMISH. 1982. Descriptions and keys for ammocoetes of lampreys from British Columbia, Canada. Can. J. Fish. Aquat. Sci. 39: 1484–1495.

SCOTT, D. P. 1957. Spawning requirements of sea lamprey. Fish. Res. Board Can. Biol. Stn. Lond. Annu. Rep. 1956–1957. Append. O.

SMITH, B. R., AND J. J. TIBBLES. 1980. Sea lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan and Superior: history of invasion and control, 1936–79. Can. J. Fish. Aquat. Sci. 37: 1780–1801.

THOMAS, M. L. H. 1961. The distribution of sea lamprey ammocoetes in the lake of eight rivers draining into the Canadian waters of Lake Superior. Fish. Res. Board. Can. MS Rep. 710: 74 p.

WAGNER, W. C., AND T. M. STAUFFER. 1962a. The population of sea lamprey larvae in East Bay, Alger County, Michigan. Pap. Mich. Acad. Sci. Arts Lett. 47: 235–245.

1962b. Sea lamprey larvae in lentic environments. Trans. Am. Fish. Soc. 91: 384–387.

Test of Biotic and Abiotic Environmental Determinants of Amphipod (*Hyalella azteca*) Preamplexus

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France, R. L. 1987. Test of biotic and abiotic environmental determinants of amphipod (*Hyalella azteca*) preamplexus. Can. J. Fish. Aquat. Sci. 44: 478–482.

Variation in reproductive behavior (preamplexus) of the amphipod *Hyalella azteca* among 10 Canadian Shield lakes in Ontario was positively correlated with water temperature, possibly through its influence on either activity patterns or diapausal endocrinology. Intensity of preamplexus was not correlated with other abiotic variables including lake pH, alkalinity, total phosphorus, or chlorophyll *a* concentration. Similarly, the complicated evolutionary "strategies" suggested by Strong involving alterations in optimal mating tactics in response to differences in intensity of fish predation, amphipod density, or habitat heterogeneity did not occur in these lakes.

La variation du comportement reproducteur (préamplexus) de l'amphipode *Hyalella azteca* dans 10 lacs du bouclier canadien (Ontario) était en corrélation positive avec la température de l'eau probablement à cause de son influence sur les régimes d'activité ou sur l'endocrinologie de la diapause. L'intensité du préamplexus n'était pas corrélée à d'autres variables abiotiques, dont le pH lacustre, l'alcalinité, le phosphore total ou la concentration de chlorophylle *a*. Par ailleurs, des modifications des tactiques d'accouplement optimales en réaction aux différences de l'intensité de la prédation par les poissons, de la densité des amphipodes ou de l'hétérogénéité de l'habitat, c'est-à-dire les « stratégies » évolutionnaires compliquées proposées par Strong, n'ont pas été observées dans ces lacs.

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Many amphipod species have precise and highly structured reproductive cycles involving complex, ritualized behavior patterns (Embody 1911). *Hyalella azteca* (Saussure) is a freshwater amphipod inhabiting many permanent bodies of water throughout North America that have mean monthly summer temperatures exceeding 10°C (Bousfield 1958). Fertilization in *Hyalella* occurs after the release of the previous brood of young and subsequent molting of the female, and is always preceeded by a period of precopulatory association or preamplexus. Because female *Hyalella* do not store sperm, preamplexus is essential to ensure the presence of a male for the next ovulation. Detailed components of mating behavior were described by Holmes (1903), Kruschwitz (1972), Strong (1973), and Borowsky (1984).

Strong (1973) suggested that duration of preamplexus in *Hyalella* was an evolutionary compromise between selective forces that lengthened or shortened the period of association. He hypothesized that the fraction of the female molt cycle spent in preamplexus, as represented by the proportion of paired individuals within field samples, would vary among lakes negatively in relation to (1) intensity of predation by visually orienting fish, (2) amphipod population density, and (3) unfavorability of habitat in terms of food supply.

Because the populations studied by Strong were from such geographically displaced and diverse lakes, the observed differences in reproductive behavior may represent other limnological factors leading to genetic isolation unrelated to the previous three biotic variables. When dealing with the subtle interactions of species, it is useful to construct rigid null hypotheses of, if not randomness, at least simplicity (Strong 1979). Therefore, three groups of abiotic variables were selected as alternative hypotheses. (1) As previous laboratory work showed that the induction of preamplexus in *Hyalella* was directly associated with temperature (de March 1977, 1978), I thought that the probability of observing mating pairs in any lake might, therefore, increase in conjunction with rising water temperature. (2) Because epibenthic algal growth and food intake are important in influencing *Hyalella* fitness (Hargrave 1970), it is conceivable that reproductive activity could also increase with several measures of system productivity such as total phosphorus and chlorophyll *a* concentration. (3) Finally, as the Haliburton–Muskoka region is affected by anthropogenic acidification (LaZerte and Dillon 1984), and shifts in water acidity are known to reduce crustacean locomotion depending on exposure history (France 1985), decreases in lake pH or alkalinity might potentially adversely effect *Hyalella* preamplexus. This could help explain the 2-wk delay in *Hyalella* recruitment observed within an acidified lake in this region (Stephenson and Mackie 1986).

Study Lakes

Specimens of *Hyalella azteca* were collected from 10 lakes (Red Chalk Lake is a double-basined lake with distinct limnological differences and is treated as two separate lakes for analysis) monitored by the Ontario Ministry of the Environment near Dorset, in the Haliburton–Muskoka region of Ontario. The lakes are located on the Precambrian Shield and are ice-covered from December to April. Water chemistry data were obtained from Dillon et al. (1987). Data on lake temperature are from Reid and Girard (1985). Status of fish populations in these lakes was assessed by H. Harvey and associates (Department of Zoology, University of Toronto). Estimates of fish population size, based on mark-and-recapture estimates, exist for three of the lakes (Harvey 1982). Relative abundances from numerous sampling techniques were calculated for fish from the other lakes (Harvey and Lee 1980). These ranged from 151 fish for Blue Chalk Lake to 909 fish for Heney Lake.

Methods

Proportions of populations undergoing preamplexus were estimated by counting the number of paired individuals in relation to the total number of adult amphipods obtained from a series of samples collected by gently dragging a scoop-like sieve across the substratum as in Strong (1973). For each lake, I sampled *Hyalella* from the littoral zone between 0.3 and 0.7 m depth over the region of densest macrophyte cover (usually *Erocaulon septangulare*), and occasionally from other areas: sand with sparse macrophytes (usually *Lobelia dortmanna*), allochthonous detritus, and organic sediment. In these lakes, as elsewhere (Hargrave 1970), most *Hyalella* inhabit this stratum of shallow water. Each lake was sampled at least three times during the reproductive season between May 30 and July 25 in 1984. After this time, adult mortality and recruitment precluded making accurate estimates of the extent of preamplexus. Amphipod densities were estimated as the mean of 5–15 samples collected with a simple corer (area = 45.6 cm^2) at the same time and sites as the scoop samples. Following gentle sieving, samples were taken to the laboratory where they were sorted live and enumerated. All plant material from the cores was thoroughly washed and frozen. Macrophytes were dried at 60°C for 48 h for biomass determinations.

As percentages of *Hyalella* in preamplexus varied from near zero to over 30%, these values were square root arcsine transformed before regression with macrophyte biomass, adult amphipod density, and temperature, respectively. To achieve homeoscadicity of variances, means of amphipod densities and macrophyte biomasses were third-root and log transformed, respectively. Additivity of proportions to obtain an overall level of preamplexus for a population was facilitated by the log $(x + 1)$ transformation. This produced values ranging from 2.301 for the main basin in Red Chalk Lake to 4.493 for Heney Lake, which were then used for regression with other limnological variables. The rate of spring temperature increase for each lake was calculated based on derivations of degree-days as in Winberg (1971), i.e. the inverse of the sum of days from 1–10°C, 10–15°C, and 15–20°C. Because of small sample sizes (i.e. 7–11 lakes), the nonparametric rank correlations, Spearman's *Rs* and Kendall's tau, were also calculated for all relationships.

The fish abundance data of Harvey (1982) and Harvey and Lee (1980) were converted to an index of predation intensity by weighting each species from 1 to 5 on their likelihood of consuming amphipods based on seasonal distributions, foraging behavior, and gut analyses described in Scott and Crossman (1973). These literature-derived, fish-specific ratings of amphipod predation agreed closely with actual analyses of gut contents of fish collected from lakes within the Dorset region (T. Stewart, Ontario Ministry of Natural Resources, Dorset Research Centre, Dorset, Ont., unpubl. data). The predation ratings were then multiplied by the relative catches and summed to obtain a total for each lake. Values ranging from 491 for Blue Chalk Lake to 4279 for Heney Lake were produced. The ordering of lakes by predation intensity was similar to that based on relative fish abundance. To account for vari-

TABLE 1. Proportion of preamplexed *Hyalella azteca* in samples from macrophyte beds in Canadian Shield lakes near Dorset, central Ontario. D, Dickie Lake; HY, Heney Lake; G, Glen Lake; GF, Gullfeather Lake; B, Buck Lake; LC, Little Clear; RC, Red Chalk Lake; BC, Blue Chalk Lake; HP, Harp Lake; CN, Crosson Lake.

	D	HY	G	GF	B	LC	RC	BC	HP	CN
Date	May 30	May 30	May 31	June 1	June 1	June 2	June 4	June 5	June 6	June 6
% preamplexed	6	18	30	8	11	15	3	15	11	8
n	34	89	92	38	54	67	69	66	71	75
Date	June 15	June 15	June 18	June 17	June 19	June 19	June 22	June 21	June 19	June 22
% preamplexed	42	41	11	33	28	23	14	21	18	36
n	57	97	186	91	36	69	71	66	57	78
Date	July 12	July 8	July 7	July 14	July 13	July 19	July 18	July 9	July 13	July 14
% preamplexed	33	38	35	24	41	26	22	33	18	36
n	67	127	147	33	73	86	74	61	33	55

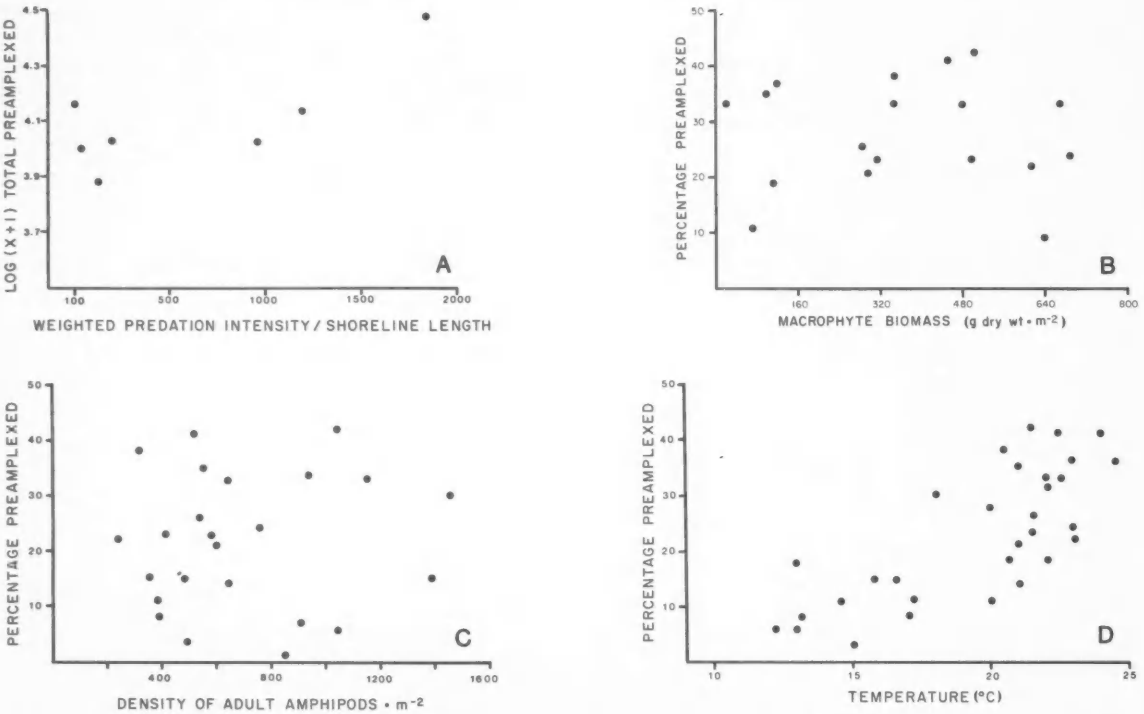

FIG. 1. Scattergrams of fish predation intensity, habitat heterogeneity, amphipod density, and lake temperature vs. *Hyalella* preamplexus.

ability in lake size, the predation intensities were divided by shoreline lengths from Nicholls et al. (1983) to calculate a concentration factor of predaceous fish within the littoral zone for each lake. A slight change of lake order was noted here, although the lakes with the two extremes in fish abundances, Blue Chalk and Heney, also had the extremes in arealy weighted predation intensity, 137.9 and 1860.4, respectively.

Results and Discussion

The proportion of *Hyalella* in preamplexus varied both among the 10 study lakes as well as within each lake on successive samplings (Table 1). Strong's (1973) three hypothetical determinants, predation intensity, macrophyte biomass, and population density, were unrelated to extent of preamplexus (Fig. 1). Of the abiotic variables, only temperature (and lake warming rate) yielded significant regression equations and correlation coefficients (Table 2).

Strong (1973) believed that because preamplexus rendered amphipods more vulnerable to fish by effectively doubling their size and slowing down their movement, predation would, through evolutionary time, select for an abbreviation of preamplexus to counteract this pressure. However, contrary to Strong's prediction, I found no difference in the extent of overlap between preamplexus and egg incubation for *Hyalella* in Dorset lakes that he would definitely have considered to be "predator stressed." In fact, the lake with by far the highest abundance of predaceous fish, Heney Lake, also had the largest

TABLE 2. Correlation coefficients of parameters examined for influence on amphipod preamplexus. Slobe (b) and correlation coefficients (r) are from parametric regression equations. Spearman's (Rs) and Kendall's tau represent rank correlation coefficients. Statistical significance: $*p < 0.05$.

Parameter	Range	n	b	r	Rs	tau
Number of fish species	6–14	10	−0.04	−0.22	−0.34	−0.20
Relative fish abundance	151–909	7	0.00	—	0.21	0.14
Predation intensity	491–4279	7	0.00	—	0.14	0.05
Predation intensity/shore length	137.9–1860.4	7	0.00	—	0.39	0.33
Macrophye biomass (g dry wt·m^{-2})	23.2–693.2	18	−0.32	−0.02	−0.12	0.05
Adult amphipod density (no·m^{-2})	264–1468	24	−0.01	0.04	0.14	0.04
Total phosphorus ($\mu g \cdot L^{-1}$)	5.71–20.70	11	0.48	0.36	0.11	0.09
Chl a ($\mu g \cdot L^{-1}$)	1.83–5.45	11	0.06	0.11	−0.23	−0.16
pH	5.65–7.23	11	−0.11	−0.09	0.05	0.02
Alkalinity ($\mu eq \cdot L^{-1}$)	58.4–202	11	0.00	—	−0.37	−0.33
Temperature (°C)	6.0–24.5	31	1.73	0.74*	0.76*	0.60*
Spring warming rate	1.25–2.85	11	0.86	0.56*	0.60*	0.55*

proportion of the amphipod population undergoing preamplexus during the reproductive season. Similarly, despite an order of magnitude higher population size estimate of fish for Crosson Lake (2453/ha) compared with both Harp (173/ha) and Red Chalk (344/ha) lakes (Harvey 1982), the total proportion of preamplexed *Hyalella* throughout the sampling period in the former was almost twice as great in the latter two lakes.

Ware (1973) found that although fish selected for larger sized *Hyalella*, susceptibility to predation was much more sensitive to amphipod behavior and activity patterns which changed with water temperature. The failure to find an inverse relationship between estimates of fish predation intensity and degree of preamplexus (Table 2) may be because the decrease in amphipod activity during this period (Adams and Greenwood 1983) more than compensated for the increased likelihood of predation caused by a size doubling.

Habitat structural complexity, as reflected by macrophyte cover, serves as an important determinant in benthic invertebrate community structure by reducing fish predator efficiency (Crowder and Cooper 1982; Gilinsky 1984). Johannes and Larkin (1961) and Ware (1972) found that risk of capture of *Hyalella* was inversely related to macrophyte or detrital cover. Therefore, if predation exerts as significant a selective force determining preamphipod amplexus as Strong hypothesized, then a direct relationship between macrophyte biomass (the inverse of prey exposure) and degree of preamplexus might be expected. This, however, did not occur in Dorset lakes (Fig. 1B). Because of this habitat complexity and the resulting unavailability of many benthic invertebrates to exploitation, together with the generally low abundances of fish, the littoral benthos in Canadian Shield lakes may be relatively unstressed by predation (Boisclair and Leggett 1985; R. L. France, unpubl. data).

The littoral zones of the Canadian Shield lakes in the present study are both structurally complex and spatially patchy. For any single occasion within any lake, there was never a difference in extent of preamplexus among the four habitat types (macrophytes, sand, organic sediment, detritus), either when they were widely spaced around the perimeter of the basin or located within a restricted area. It seems doubtful that Strong's hypothesis concerning male competition for mates in relation to habitat favorability and female feeding efficiency is important in influencing preamplexus in these lakes. Thompson and Moule (1983) also found that substrate heterogeneity was not as important a determining factor of amphipod preamplexus as had been previously suggested.

Because of the suggested disadvantages to long periods of preamplexus due to fish predation, Strong suggested that under conditions of high male availability, the female would control the duration of association by restricting the period during which she would accept a male partner to the last portion of her molt cycle. However, the expectation of an inverse relationship between population density and preamplexus was not realised in Dorset lakes (Fig. 1C). This may be because if the absolute number of both competing males and available females increases in proportion within a population, then any counteracting shifts in duration of preamplexus caused by these two variables (Ward 1983) would be expected to be cancelled out.

The increase in preamplexed *Hyalella* throughout the spring (Table 1) in relation to increasing water temperature (Fig. 1D) is consistent with de March's (1977) findings that induction of preamplexus was progressively lower at temperatures below 20°C. From this work, she believed that for temperate zone populations, spring light levels are sufficient for preamplexus but *Hyalella* is "held back" from reproducing by low temperatures. The significant positive relationship between extent of preamplexus and rate of temperature increase in Dorset lakes is supportive of de March's (1978) hypothesis that preamplexus may vary yearly within a lake due to the spring warming cycle and geographically among lakes in relation to latitudinal thermal differences. Due to small sample sizes and sporadic, occasionally single, sampling periods, Strong (1973) did not detect the importance of temperature on preamplexus in his populations. However, the fact that preamplexus was always highest in the hot spring, perennially heated to between 20 and 40°C, is consistent with the present argument that preamplexus is temperature dependent.

The functional basis behind the relationship of temperature to *Hyalella* preamplexus is unknown, but two mechanisms, one environmental and one physiological, can be hypothesized. (1) Because tactile communication and not secretion of sexual pheromones precipitates preamplexus in *Hyalella* (Strong 1973), and level of swimming activity is determined by temperature (Ware 1973), pairings may be controlled by the effect of temperature on locomotion. (2) The positive relationship between *Hyalella* preamplexus and lake temperature may reflect a reduction in the number of days between successive matings with increasing temperature (de March 1978), probably in conjunction with increased frequencies of molting (Geisler 1944). Ward (1985) also found seasonal variation in du-

ration and proportion of animals engaged in preamplexus and suggested that water temperatures influenced brood development time in relation to length of the female molt cycle. The temperature-dependent release of antidiapause and growth-regulating hormones has been established for other invertebrates (Way and Hopkins 1950) and may regulate female *Hyalella's* acceptance of a male partner in relation to the stage of her molt cycle.

Experiments by Strong (1973) on the progeny of amphipods collected from Oregon lakes indicated that differences in the proportion of animals engaging in preamplexus were heritable. This is in contrast with *Hyalella* collected from Dorset lakes where the tendency to preamplex seems opportunistic, dependent on the probability of chance encounters. This may be because the amphipods investigated in this study were from a group of lakes located within a small area where the likelihood of genetic exchange through transportation by waterfowl (Rosine 1956; Maguire 1963) is greater than among the populations studied by Strong.

Acknowledgments

R. Reid and N. Yan are thanked for their helpful suggestions on initial site selection and P. Dillon for providing both facilities at the Dorset laboratories and background chemical data. Use of unpublished fish data by H. Harvey is greatly appreciated. M. Stephenson assisted in designing the sampling apparatus. Encouraging comments were received in reply from both D. Strong and B. de March. Constructive criticisms of the manuscript were provided by R. Baker, N. Collins, N. Yan, P. Stokes, E. Bousfield, and S. Rang. This study was funded in part by an OGS scholarship through the Department of Botany, University of Toronto, and by an NSERC strategic grant to P. Stokes, N. Collins, and J. VanLoon.

References

ADAMS, J., AND P. J. GREENWOOD. 1983. Why are males bigger than females in pre-copula pairs of *Gammarus pulex*? Behav. Ecol. Sociobiol. 13: 239–241.

BOISCLAIR, D., AND W. C. LEGGETT. 1985. Rates of food exploitation by littoral fishes in a mesotrophic north-temperate lake. Can. J. Fish. Aquat. Sci. 42: 556–566.

BOROWSKY, B. 1984. The use of the males' gnathopods during precopulation in some gammaridian amphipods. Crustaceana 47: 245–250.

BOUSFIELD, E. L. 1958. Freshwater amphipod crustaceans of glaciated North America. Can. Field-Nat. 72: 55–113.

CROWDER, L. B., AND W. E. COOPER. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63: 1802–1813.

DE MARCH, B. G. E. 1977. The effects of photoperiod and temperature on the induction and termination of reproductive resting stage in the freshwater amphipod *Hyalella azteca* (Saussure). Can. J. Zool. 55: 1595–1600.

1978. The effects of constant and variable temperature on the size, growth, and reproduction of the freshwater amphipod *Hyalella azteca* (Saussure). Can. J. Zool. 56: 1801–1806.

DILLON, P. J., K. H. NICHOLLS, W. A. SCHEIDER, N. D. YAN, AND D. S. JEFFRIES. 1987. Lakeshore capacity study: trophic status component summary report. Ontario Ministry of Housing, Toronto, Ont. (In press)

EMBODY, G. C. 1911. A preliminary study of the distribution, food, and reproductive capacity of some freshwater amphipods. Int. Rev. Gesamten Hydrobiol. Biol. Suppl. 3: 1–33.

FRANCE, R. L. 1985. Low pH avoidance by crayfish (*Orconectes virilis*): evidence for sensory conditioning. Can. J. Zool. 63: 258–262.

GEISLER, F. S. 1944. Studies on the post-embryonic development of *Hyalella azeteca* (Saussure). Biol. Bull. 86: 6–22.

GILINSKY, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology 65: 455–468.

HARGRAVE, B. T. 1970. Distribution, growth, and seasonal abundance of *Hyalella azteca* (Amphipoda) in relation to sediment microflora. J. Fish. Res. Board Can. 27: 685–699.

HARVEY, H. H. 1982. Population responses of fish in acidified waters p. 227–244. *In* R. E. Johnson [ed.] Acid rain/fisheries. Proc. Int. Symp. Cornell University, Ithaca, NY.

HARVEY, H. H., AND C. LEE. 1980. Fish populations in the calibrated watersheds of Muskoka–Haliburton. Ontario Ministry of the Environment, Manuscript Report. (Available from H. Harvey, Department of Zoology, University of Toronto, Toronto, Ont.)

HOLMES, S. J. 1903. Sex recognition among amphipods. Biol. Bull. 5: 288–292.

JOHANNES, R. E., AND P. A. LARKIN. 1961. Competition for food between redside shiners (*Richardsonius balteatus*) and rainbow trout (*Salmo gairdneri*) in two British Columbia lakes. J. Fish. Res. Board Can. 18: 203–220.

KRUSCHWITZ, L. G. 1972. An analysis of reproductive behavior patterns of the amphipod *Hyalella azteca*. Am. Zool. 12: 658–659.

LAZERTE, B. D., AND P. J. DILLON. 1984. Relative importance of anthropogenic versus natural sources of acidity in lakes and streams of central Ontario. Can. J. Fish. Aquat. Sci. 41: 1664–1677.

MAGUIRE, B. 1963. The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. Ecol. Monogr. 33: 161–185.

NICHOLLS, A., R. REID, AND R. GIRARD. 1983. Morphometry of the Muskoka–Haliburton study lakes. MOE Data Rep. 83/3. (Available from Ontario Ministry of the Environment, Dorset, Ont.)

REID, R. A., AND R. GIRARD. 1985. Temperature and oxygen data for the Muskoka–Haliburton Study lakes (1983–1984). MOE Data Rep. 85/2. (Available from Ontario Ministry of the Environment, Dorset, Ont.)

ROSINE, W. 1956. On the transport of the common amphipod *Hyalella azteca* in South Dakota by the mallard duck. Proc. S.D. Acad. Sci. 35: 203.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.

STEPHENSON, M., AND G. L. MACKIE. 1986. Lake acidification as a limiting factor in the distribution of the freshwater amphipod *Hyalella azteca*. Can. J. Fish. Aquat. Sci. 43: 288–292.

STRONG, D. R. 1973. Amphipod amplexus, the significance of ecotypic variation. Ecology 54: 1383–1388.

1979. Null hypotheses in ecology, p. 245–260 *In* E. Saarinen [ed.] Conceptual issues in ecology. D. Reidel Publishing Co., Boston, MA.

THOMPSON, D. J., AND S. J. MOULE. 1983. Substrate selection and assortive mating in *Gammarus pulex* L. Hydrobiologia 99: 3–6.

WARD, P. I. 1983. Advantages and a disadvantage of large size for male *Gammarus pulex* (Crustacea: Amphipoda). Behav. Ecol. Sociobiol. 14: 69–76.

1985. The breeding behavior of *Gammarus duebeni*. Hydrobiologia 121: 45–50.

WARE, D. M. 1972. Predation by rainbow trout (*Salmo gairdneri*): the influence of hunger, prey density, and prey size. J. Fish. Res. Board Can. 29: 1193–1201.

1973. Risk of epibenthic prey to predation by rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 30: 787–797.

WAY, M. J., AND B. A. HOPKINS. 1950. The influence of photoperiod and temperature on the induction of diapause in *Diataraxia oleracea* (Lepidoptera). J. Exp. Biol. 27: 365–376.

WINBERG, G. G. 1971. Methods for the estimation of production of aquatic animals. Academic Press, New York, NY. 161 p.

LETTERS AND COMMENTS/LETTRES ET COMMENTAIRES

Comment on "Influence of Sea Temperature upon the Numbers of Grilse and Multi-Sea-Winter Salmon (*Salmo salar*) Caught in the Vicinity of the River Dee (Aberdeenshire)" by Martin and Mitchell (1985)

I have discovered several faults in a recently published paper on salmon and sea temperature (Martin and Mitchell 1985). The faults introduced considerable confusion into an otherwise interesting paper and are especially worth clarifying because of the authors' stated intention (p. 1514) to publish another paper on the subject.

First, there were errors of logic in the grilse and MSW salmon regression equations. The value of these models lies in their ability to predict the number of grilse or MSW salmon returning "next year" (year "*t*"), and Martin and Mitchell asserted that their models "could have been used predictively" (p. 1520). However, both the grilse models (equations 1, 3, and 4) and the MSW salmon models (equations 2, 5, and 6) included the weight of fish in the year "*t*" as well as the average sea temperature in the year "*t*". Obviously, these variables cannot be included in any model intending to make predictions for the year "*t*", since they could only be measured after the salmon runs in year "*t*".

Second, the symbols of "actual" and "predicted" catch numbers in the graphs for grilse (Fig. 4) and MSW salmon (Fig. 5) are reversed. As published, the "predicted" numbers exhibit much more variance than the "actual" number, whereas the opposite would be expected. I estimated the numbers from the graphs and compared these with the data from 1951 to 1972 published in Table 5. I found the "actual" numbers estimated from the graphs to agree extremely well with the "predicted" numbers in the table and vice versa.

Finally, two quite different objectives seemed to be involved in the research but not clearly distinguished in the paper. The first objective, as stated in the abstract, was to examine the "possible influence of sea temperature upon the age of return of Atlantic salmon (*Salmo salar*)." The opening paragraph indicated the scientific facts motivating the study:

> The factors that influence the sea age at which Atlantic salmon (*Salmo salar*) return to spawn are not fully understood. Grilse (one-sea-winter salmon) predominate in the spawning runs of the short spate rivers of the Scottish west coast; salmon (multi-sea-winter (MSW) fish) are an important component of the runs in the larger east coast rivers such as the Aberdeenshire Dee. . . . major long-term trends in the *relative abundance* [italics mine] of grilse and MSW salmon (George 1982a) are also evident and cannot be explained in local terms.

It is clear that the scientific interest lies in determining if, and how much, sea temperature influences the proportion of a smolt cohort that make the ecophysiologic "decision" to spawn first as grilse or MSW salmon.

The second objective, suggested in the title and dominating the quantitative analysis, was in "quantifying the relationship between grilse, salmon, their respective mean weights, and sea temperature." The motivation for this objective lies in the practical exploitation and management of the salmon stock, particularly in making annual predictions of the numbers of spawning grilse and MSW salmon.

Different analytical methods should have been used to address the separate objectives. An index of relative abundance, such as that presented by the authors (the percent of a smolt cohort that returns as MSW salmon), correlated with sea temperature would have effectively revealed the possible influence of sea temperature on the proportion of a smolt cohort to spawn first as grilse or MSW salmon. Martin and Mitchell presented graphs of percent MSW salmon (Fig. 1a) and sea temperature (Fig. 1b) that only suggested a correlation; publishing the actual correlation coefficient would have been more informative. The correlation coefficients of sea temperature with absolute numbers of grilse and MSW salmon presented (in Table 4) may be significantly affected by the complicating factor of annual variations in smolt cohort or total spawning stock size. Thus, the influence of sea temperature on the proportion of a smolt cohort to spawn first as grilse or MSW salmon cannot be directly interpreted from these.

Although this paper contained interesting data and ideas, the failure to distinguish clearly the different objectives, use the most appropriate methods to achieve them, and the errors in the models and graphs diminished its readability and its contribution to fishery science. I hope future papers relating to the influence of sea temperature on Atlantic salmon will avoid similar problems — Richard A. Evans, *Department of Natural Resources, Fernow Hall, Cornell University, Ithaca, NY 14853, U.S.A.* (J8881a)

References

MARTIN, J. H. A., AND K. A. MITCHELL. 1985. Influence of sea temperature upon the numbers of grilse and multi-sea-winter Atlantic salmon *(Salmo salar)* caught in the vicinity of the River Dee (Aberdeenshire). Can. J. Fish. Aquat. 42: 1513–1521.

GEORGE, A. F. 1982a. Cyclical variations in the return migrations of Scottish salmon by sea-age 1970–1976. M. Phil. thesis, Open University, Milton Keynes, England. 365 p.

Reply to Comments by R. A. Evans

Evans is correct on one point, his second. The symbols for actual and predicted numbers in Fig. 4 and 5 of Martin and Mitchell (1985) were interchanged by the *Journal*. I regret any difficulties this unfortunate printing error may have caused.[1] I

[1]The *Journal* apologizes to Drs. Martin and Mitchell for introducing the error and to any reader confused by it — *Editor*.

do not, however, accept the criticism implicit in his other statements.

The purpose of the paper was to draw attention to the strong possibility that sea temperature is influential in determining the sea age of salmon. An historical data set was used. Historical because the temperature data set terminated in 1972 (p. 1514) when the temperature recording equipment at Grimsey malfunctioned. It has never been replaced. As these data can play no future role in estimating the number of fish returning in any year, the regression equations were not designed for that purpose. The use of the word "predict" (p. 1520), coupled with the use of the same word on p. 1518, must be seen in context viz that of the validation of the regression equations.

However, there appears to be no inherent difficulty in producing regression equations as a forecasting tool if required. The salmon regression equation (2) on p. 1518 needs only the removal of the salmon weight term with the loss of 3–4% of the variance. It should be noted that the temperature term is for the previous year. The grilse regression equation (1) is somewhat different, a new temperature term being needed. The monthly data set for Grimsey has not been made available to us. However, we have the February and May monthly values for the period 1880–1941. Both show correlation coefficients with grilse catch number comparable with the annual value ($R = -0.42$, -0.45, and -0.50, respectively, for the February, May, and annual values).

Using the February monthly mean values, the following regression equation is obtained:

$$G_t = 0.544 + 0.259G_{t-1} + 0.153G_{t-2} + 0.028G_{t-3} + 0.416G_{t-4} - 0.028T_{Ft}$$

where the terms have the same meaning as in equation (1). The multiple correlation coefficient was 0.678. The high correlations between the annual temperature value and the February and May temperature values for the period 1880–1941 allowed us to speculate that the minimum temperatures associated with winter and spring were possibly the most relevant (p. 1520). The difficulty for the future does not lie in producing a suitable regression equation as a forecasting tool but in obtaining an accurate, appropriate, and continuing temperature data set.

Evans postulates that the value of the regression equations lies in their ability to predict and presumably, from his comments, only to do so. I do not agree. Regression equations were used as a technique by which grilse and salmon catch numbers could be treated both as separate entities but yet be linked through a common temperature term. They were therefore able to deal with the kind of issue raised by Evans in his important third point.

The correlation coefficient of sea temperature with percentage MSW salmon was $R = 0.61$, higher than the value for grilse ($R = -0.425$) or MSW salmon ($R = 0.295$). We did not use an index of relative abundance, however, in any analytical method because it is too limiting and reveals too little of what is occurring. Essentially, using a percentage allows for only two solutions: a smolt returns as a grilse or as a MSW salmon. Using actual catch numbers allows for a third possibility: the fish does not return at all. This is important because, while the use of an index of relative abundance is sufficient to deal with problems caused by the effect of annual variation in smolt cohort or total spawning stock size, it is insufficient to deal with other problems. For example, without catch numbers it would be impossible to discern whether an increased percentage of grilse in the catch figures was due to an increase in actual grilse catch numbers or to a decrease in salmon catch numbers. The latter could be due to increased mortality in the second year at sea rather than being due to the ecophysiological decision to spawn as a grilse.

It seems to have escaped Evans' observation that the temperature term in the grilse regression equation (1), $T_{(t)}$, is the same as the temperature term in the salmon regression equation (2), $T_{(t-1)}$. The time t refers to the year of return of grilse and MSW salmon in their respective regression equations. Two-sea-winter salmon return 1 yr later than grilse. By linking the two regression equations, we showed that, for any year, the temperature correlated negatively with grilse catch numbers and correlated positively with MSW salmon catch numbers, both from the same smolt year — J. H. A. Martin, *Marine Laboratory, P.O. Box 101, Victoria Road, Aberdeen.*

(J8881b)

References

MARTIN, J. H. A., AND K. A. MITCHELL. 1985. Influence of sea temperature upon the numbers of grilse and multi-sea-winter Atlantic salmon (*Salmo salar*) caught in the vicinity of the River Dee (Aberdeenshire). Can. J. Fish. Aquat. 42: 1513–1521.

ANNOUNCEMENTS / AVIS

The National Shellfisheries Association (NSA) is an international association of scientists, management officials, and members of industry that is deeply concerned and dedicated to the formulation of ideas and promotion of knowledge pertinent to the biology, ecology, production, economics, and management of shellfish resources. The membership, exceeding 700, includes the United States, Canada, and 18 other nations.

The 79th Annual Convention of NSA will be held in Halifax, Nova Scotia, from August 9 to 13, 1987. Questions about local arrangements can be directed to Brian Muise, Chairman, Convention Co-ordinating Committee, Nova Scotia Department of Fisheries, P.O. Box 2223, Halifax, N.S. B3J 3C4. Telephone: (902) 424-4560.

Roger Mann, Program Chairman, welcomes your suggestions for technical sessions and special symposia. The January 1987 NSA Newsletter will contain abstract forms and instructions. Abstracts will be due April 1, 1987. Please direct your comments or questions on the program to Dr. Roger Mann, College of William and Mary, Virginia Institute of Marine Science, Gloucester Pt., VA 23062, USA. Telephone: (904) 642-7360.

New members are welcome and encouraged to attend.

La *National Shellfisheries Association* (NSA) est une société internationale regroupant des scientifiques, des gestionnaires et des membres de l'industrie qui s'intéressent beaucoup et se consacrent à la formulation d'idées et à la diffusion des connaissances sur la biologie, l'écologie, la production, les aspects financiers et la gestion et matière de mollusques et de crustacés. La société regroupe plus de 700 membres venant des États-Unis, du Canada et de 18 autres pays.

Le 79^{e} Congrès annuel de la NSA se tiendra à Halifax (Nouvelle-Écosse) du 9 au 13 août 1987. Toute question concernant les arrangements relatifs au congrès doit être adressée à Brian Muise, Président, Comité de coordination du Congrès, Ministère des Pêches de la Nouvelle-Écosse, C.P. 2223, Halifax (N.-É.) B3J 3C4. Téléphone : (902) 424-4560.

Roger Mann, le président de la programmation, acceptera avec plaisir vos suggestions en matière de séances techniques ou de colloques spéciaux. Le Bulletin de la NSA de janvier 1987 contiendra des formulaires de présentation de résumés ainsi que des instructions pour leur rédaction. Ces résumés devront être reçus pour le 1er avril 1987. Veuillez faire parvenir vos commentaires et questions au sumet du programme à Roger Mann, Ph.D., College of William and Mary, Virginia Institute of Marine Science, Gloucester Pt., VA 23062, USA. Téléphone : (904) 642-7360.

Nous souhaitons la bienvenue aux nouveaux membres et nous les encourageons à assister au Congrès.

CORRECTIONS TO RECENT PUBLICATIONS
CORRECTIONS SUR RÉCENTES PUBLICATIONS

VOLUME 43, No. 5 — letter by D. Mathur, W. H. Bason, E. J. Purdy, Jr., and C. A. Silver: *Reply to "In defense of the instream flow incremental methodology" by D. J. Orth and O. E. Maughan.*

Page 1094: The reference "Shirvell, C. S. 1984. Review of incremental flow type methodology for assessing the effects of reduced stream flows on fish populations. Can. Tech. Rep. Fish. Aquat. Sci. No. 1234: 84 p." never has been and never will be published; regretably this "document" was circulated as a preprint bearing a dummy report number. The correct reference is "Shirvell, C. S. 1986. Pitfalls of physical habitat simulation in the instream flow incremental methodology. Can. Tech. Rep. Fish. Aquat. Sci. 1460: 68 p."

COMING NEXT MONTH / À PARAÎTRE LE MOIS PROCHAIN

Articles

Grant, W. S., C. I. Zhang, T. Kobayashi, and G. Ståhl. Lack of genetic stock discretion in Pacific cod (*Gadus macrocephalus*)

Fahnenstiel, G. L., and D. Scavia. Dynamics of Lake Michigan phytoplankton: primary production and growth

Fahnenstiel, G. L., and D. Scavia. Dynamics of Lake Michigan phytoplankton: recent changes in surface and deep communities

Nalepa, T. F. Long-term changes in the macrobenthos of southern Lake Michigan

Beamish, R. J., and J. H. Youson. Life history and abundance of young adult *Lampetra ayresi* in the Fraser River and their possible impact on salmon and herring stocks in the Strait of Georgia

Freedman, B., and T. A. Clair. Ion mass balances and seasonal fluxes from four acidic brownwater streams in Nova Scotia

Mills, E. L., D. V. Widzowski, and S. R. Jones. Food conditioning and prey selection by young yellow perch (*Perca flavescens*)

Seeb, J. E., L. W. Seeb, D. W. Oates, and F. M. Utter. Genetic variation and postglacial dispersal of populations of northern pike (*Esox lucius*) in North America

Kieser, R., T. J. Mulligan, N. J. Williamson, and M. O. Nelson. Intercalibration of two echo integration systems based on acoustic backscattering measurements

Campton, D. E., and F. M. Utter. Genetic structure of anadromous cutthroat trout (*Salmo clarki clarki*) populations in the Puget Sound area: evidence for restricted gene flow

Welch, D. W. Frequency domain filtering of age-structured population data

Paloheimo, J. E., and R. R. Fulthorpe. Factors influencing plankton community structure and production in freshwater lakes

McQueen, D. J., and D. R. S. Lean. Influence of water temperature and nitrogen to phosphorus ratios on the dominance of blue-green algae in Lake St. George, Ontario

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